

**THE ECOLOGY OF ADAPTIVE RADIATION OF
DABBLING DUCKS (*ANAS* SPP.)**

by

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ABSTRACT

The ecological theory of adaptive radiation proposes that three processes are responsible for the evolution of a single ancestor into a clade of species: divergence in phenotype between contrasting environments; divergence in phenotype caused by negative interspecific interactions; and ecological speciation. I tested for evidence of these processes among sympatric dabbling ducks (*Anas* spp.), a putative adaptive radiation.

Divergent selection between environments requires a trade-off in the ability of phenotypes to exploit resources in different environments. I tested whether variation in bill morphology imposes a performance trade-off when ducks filter-feed in environments containing different size-frequency distributions of prey and indigestible detritus. Experiments demonstrated that ducks could avoid ingesting detritus when prey and detritus differ in size. Foraging models based on filter-feeding biomechanics predict prey size selection causes a decline in filtration rates and that the form of this trade-off depends on interspecific differences in bill morphology. To test these models, I used them to predict the results of manipulative foraging experiments on 2 species reported in the literature. There was overall agreement between model predictions and reported differences in filtration rates, particle retention probabilities and ingestion rates, both between species and due to variation in prey size, presence of detritus and surgical manipulation of bill morphology. Extension of these models to five additional species predicts that interspecific variation in the foraging trade-off should result in interspecific partitioning of prey by size when detritus is present.

To determine if phenotypic divergence is the result of negative interspecific interactions, I tested for a negative correlation between frequencies of interspecific aggression and phenotypic divergence. Comparison of observed frequencies to the predictions of a null model indicated aggression differed between species pairs. Divergence in body size, body length, lamellar density and divergence of species along a prey size axis predicted by the biomechanical models were all negatively correlated with frequency of aggression, even after controlling for phylogenetic distance. Variation in aggression accounted for by phenotype and phylogeny were additive, indicating ecology and evolutionary history contribute independently to species interactions. These results provide evidence that dabbling ducks represent an adaptive radiation.

DEDICATION

For Sandra

Because she gave the most

and expected the least

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The beak of a shoveller-duck is a... beautiful and complex structure.

Charles Darwin, *Origin of Species*, p. 286

Data are treacherous when offered in support of explanations free of theory. Do not trust such explanations, no matter how much data seems to support them. Without the theory, it is too easy to confuse scales and to be unaware of what variables need to be measured.

M.L. Rosenzweig, *Species Diversity in Space and Time*, p. 5-6

CHAPTER 1 INTRODUCTION

1.1 Introduction

The ecological theory of adaptive radiation proposes to explain the rapid divergence of a single ancestral species into a group of species distinguishable by their ecological differentiation. Adaptive radiation is remarkable not only because it accelerates speciation rates and leads to a diversity of phenotypic traits selected to exploit different environments, but also for its potential ubiquity. Currently there is no way to estimate, *a priori*, the proportion of extant species that have been produced through the process of adaptive radiation, but it may account for the majority of extant and extinct species. A plausible estimate of the proportion of extant species will be possible only after a thorough examination of many putative cases.

The ecological theory of adaptive radiation represents a major synthesis of ecological and evolutionary theory and provides a mechanistic foundation for insight into the dynamics determining the diversity of species on Earth. Understanding these dynamics is an old problem with new urgency. As the impact of humans on the Earth's environment grows, an increasing number of species are becoming endangered, while fewer species appear to benefit from human activity. If species in a candidate adaptive radiation fall into both groups, the difference in population trajectories may be explained by species' ecological differences. Consequently, the interests of evolutionary ecologists studying adaptive radiation have much in common with the interests of conservation biologists.

Of the many radiations that have been proposed, only a few are generally accepted examples of adaptive radiation (Schluter 2000), such as the Galapagos finches, the Caribbean *Anolis* lizards, the Hawaiian silverswords, and the north-temperate columbines (*Aquilegia* spp.). The majority of candidate radiations are lacking evidence that they are adaptive. Of these, none has been on the candidate list longer than the waterfowl (Anatidae). Their listing coincided with the development of the idea of evolution itself.

The family Anatidae contains approximately 150 species of swans, geese, and ducks and its members are found on every continent except Antarctica. Morphological differences between species are most evident with respect to their size, posture, colouration and bill morphology. The implications of variation in bill morphology for dictating the foraging ecology of ducks and geese

was first suggested by Charles Darwin (1998). Darwin (1998) used the anatid bill as an example of how small changes in form of the lamellae could allow for the evolution of a goose specialized for grazing, from a duck specialized for filter-feeding (or vice-versa). He noted that extant species of waterfowl exhibited an almost continuous range of variation in lamellar form between these two ecological extremes. Darwin (1998 p. 288) argued this spectrum indicated that small changes to the lamellae could occur without sacrificing the bill's utility for foraging:

We thus see that a member of the duck family, with a beak constructed like that of the common goose and adapted solely for grazing, or even a member with a beak having less well-developed lamellae, might be converted by small changes into a species like the Egyptian goose, -- this into one like the common duck -- and lastly into one like the shoveller, provided with a beak almost exclusively adapted for sifting in the water; for this bird could hardly use any part of its beak, except the hooked tip, for seizing or tearing solid food.

It was Darwin's opinion that at each point along the radiation from ancestor to ducks and geese, the unique lamellae would 'each [be] of service to its possessor'. Consequently, his argument contains the central idea of adaptive radiation: the divergence of a single ancestral species into a group of species distinguishable by their degree of ecological differentiation. The purpose of this thesis is to test whether Darwin's ducks do indeed represent an adaptive radiation. In this chapter, I review the central processes of adaptive radiation and establish what evidence is necessary to confirm that these processes are operating. I then review the dabbling duck (*Anas* spp.) literature in the context of these criteria to identify gaps in the evidence necessary to determine if dabbling ducks radiated as a result of adaptive processes. Based on a synthesis of this evidence, I propose a research plan to address these knowledge gaps. At the end of the chapter, I outline the following chapters of the thesis.

1.2 The Ecological Theory of Adaptive Radiation

The ecological theory of adaptive radiation was recently reviewed and updated by Schluter (2000). The following briefly summarizes the major points of his review. Readers interested in a more thorough discussion of the concepts and literature should refer to Schluter's review.

The ecological theory of adaptive radiation is composed of three processes: divergent selection due to negative interspecific interactions, divergent selection between environments and ecological speciation. In the absence of competition, individuals should prefer to utilize resources and environments that confer the highest fitness (Rosenzweig and Abramsky 1986). As

the abundance of preferred resources are depleted, some individuals are forced to utilize less preferred, but more abundant, resources. Alternatively, individuals may continue to use the same resource, but acquire them from less preferred environments. These individuals then become subject to new selection pressures imposed by use of the less preferred environment or resource. Competition was originally thought to result from depletion of resources, but the theory can accommodate other negative interactions (see review by Wootton 1994) that lead to divergent selection as well, such as apparent competition (Holt and Lawton 1994) and antagonistic interference (Ebersole 1985). In the remaining discussion, I refer frequently to differences between resources, but these differences may be reflected in the types of environments in which resources are found or to differences in the resources themselves.

The term 'preferred' makes a tacit link between divergent selection due to differences between environments and divergent selection due to competition. For both of these processes to lead to divergent selection, there must be trade-offs in the ability of individuals with different phenotypes to exploit different resources (Doebeli 1996; Taper and Case 1992). Performance trade-offs create variation in fitness between phenotypes because selection to increase fitness using a less preferred resource must come at the cost of reduced fitness using preferred resources. Performance trade-offs also stabilize competitive interactions and allow species coexistence because individuals with one phenotype can exploit some resources more efficiently than individuals with different phenotypes. Consequently, performance trade-offs allow the evolution of a competitive refuge through resource partitioning.

Ecological speciation is the final process of adaptive radiation and occurs as a consequence of divergent natural selection (Schluter 2001). There are many speciation models, but two general categories are by-product speciation and competitive speciation (see review by Rice and Hostert 1993). In by-product speciation, reproductive isolation arises as an indirect result of natural selection in different environments, which creates premating or postmating barriers to successful reproduction. Reproductive isolation is not selected for directly, but results due to selection acting independently in different environments to produce genetically incompatible populations. In competitive speciation reproductive isolation is selected for directly in response to reduced fitness of hybrid offspring (e.g., Rundle et al. 2000). In these models assortative mating is under natural selection because the phenotypes of hybrid offspring are less efficient at exploiting available resources. Sexual selection can play a role in both mechanisms (Schluter 2000).

1.3 Criteria for Testing Candidate Radiations

To be accepted as an adaptive radiation, there are five general categories of evidence that must be provided. Within each category, the type of evidence required may vary depending on the type of pattern being tested. Failure to satisfy any of these categories infers a candidate radiation was not caused by adaptive processes. The only exception is evidence of divergent selection due to competition. Negative interactions can occur between species for reasons other than competition and still lead to divergent selection. However, some form of negative interaction must be demonstrated.

1.3.1 Common Ancestry

Adaptive radiation involves the divergence of an ancestral lineage into multiple, descendent lineages. Consequently, tests are best conducted on monophyletic clades. Testing the predictions of adaptive radiation is more difficult if descendent species are excluded. For example, two species may not compete with each other, but do compete with another species with an intermediate phenotype. If the intermediate species is excluded, tests may conclude there is no evidence of competition. Although it is not necessary that every descendent of a common ancestor be included in tests of adaptive radiation, some justification should be given for excluding species. Reasonable grounds for exclusion include wide geographical separation, suggesting independent evolution, or extreme differences in ecology that preclude useful comparisons between phenotypes.

1.3.2 Genetic Basis of Phenotypic Traits

The type of evidence required to satisfy this criteria will depend on the pattern being investigated. At its most general, this criteria requires that phenotypic traits are heritable in order to be subject to natural selection. When testing patterns of divergent character displacement between allopatric and sympatric populations (see below), the differences in phenotypic means between populations must have a genetic basis as well. Common garden experiments can provide evidence of genetic determination for allopatric populations by controlling for the environmental component of phenotypic variation. Independent evidence is not needed when phenotypic differences exist in sympatry, because these populations already share the same environment.

1.3.3 Divergent Selection Between Environments

Evidence is needed that selection is indeed divergent between environments and that each species is better suited to the environment it inhabits. The basis of such evidence is the demonstration of a performance trade-off imposed by the interaction between phenotype and environment. Evidence can come from reciprocal transplant experiments, tests that explicitly link performance in different environments to phenotype, and direct measurement of selection in the field.

1.3.4 Divergent Selection due to Negative Interspecific Interactions

Traditionally, phenotypic divergence was thought to be due primarily to competition for resources. More recently, additional mechanisms of negative interspecific interactions have been proposed that may also lead to phenotypic divergence, such as interference competition (Adams 2004), apparent competition due to species interactions via a shared predator (Abrams 2000; Brown and Vincent 1992; Doebeli and Dieckmann 2000; Holt 1977) or intra-guild predation (Holt and Polis 1997).

Competition resulting from depletion of shared resources is assumed to lead to phenotypic divergence. Consequently, evidence is required that species compete and that competition is negatively correlated with differences in phenotype. The most common evidence comes from observation of patterns of divergent character displacement. This class of evidence includes patterns in which species' phenotypes differ more in sympatry than in allopatry (Brown and Wilson 1956), patterns of trait over-dispersion and patterns of species-for-species matching. Trait over-dispersion occurs when species' phenotypic traits are more different than expected at random (Strong et al. 1979). Species-for-species matching occurs when the distribution of species' phenotypic traits are similar between independently evolving communities occupying similar environments (Schluter 1990). Each case must pass a sub-set of additional criteria: differences in phenotypic means between sympatric and allopatric populations must have a genetic basis; patterns differ from predictions of null models; differences in phenotype are due to evolutionary shifts rather than species sorting; differences in resource use are linked with differences in phenotype; differences in phenotype must be robust to environmental differences between sites of sympatry and allopatry; and there must be independent evidence of interspecific competition.

Evidence from character displacement is problematic, however, for two reasons. First, statistical tests that identify patterns of character displacement are generally weak (Losos et al.

1989) and patterns are easily interpreted only when there is a linear relationship between a single trait and resource utilization. Consequently, negative results may be equivocal and other evidence should be sought. Second, the role of competition is implied rather than tested directly. More rigorous tests incorporate explicit measures of competitive ability. Some tests have predicted the mean phenotype of species given the abundance of resources and measures of phenotypic performance exploiting different resources (e.g., Schluter and Grant 1984). Other tests have shown experimentally that morphological similarity between species leads to stronger competition (e.g., Schluter 1994). An alternative test would compare empirical measures of competition between species to overlap in resource preference predicted from an understanding of how morphology determines resource exploitation.

1.3.5 Ecological Speciation

Ecological speciation is the least understood and the least frequently tested process. In general, tests should show a relationship between strength of reproductive isolation and extent of ecological divergence. Tests of by-product speciation could compare rates of evolution of reproductive isolation between regions differing in frequency and strength of divergent natural selection. Tests of competitive speciation require evidence that ecological interactions affect the fitness of hybrids (e.g., Schluter 1994). Competitive speciation is also the most likely process if speciation was sympatric. Demonstration that traits involved in premating isolation evolved in parallel between similar environments provides the strongest evidence of ecological speciation (e.g., Rundle et al. 2000). The primary alternative to ecological speciation is genetic drift between allopatric populations, which should increase with time since divergence. If species prefer to mate with ecologically similar, but more distantly related, species rather than with ecologically different, but more related species, then ecology is a greater barrier to gene flow than relatedness.

1.4 Review of the Evidence for Adaptive Radiation of Dabbling Ducks

The cause of the radiation of dabbling ducks, indeed of waterfowl in general, has received little integration of the three major fields of study: ecology, trait utility (i.e. functional morphology) and evolution. Only a few authors have even considered waterfowl within the context of adaptive radiation. Darwin (1998), and especially Lack (1971; 1974), thought the radiation of waterfowl was due to variation in bill morphology, which allowed species to exploit different resources, but their work was largely descriptive. Zweers and Vanden Berge (1997) and

Zweers et al. (1997) proposed a hypothetical phylogeny for waders (Charadriiformes) and waterfowl based on adaptive transitions in the functional morphology of the trophic apparatus. Their phylogeny links diversification of lineages with major changes in morphology and is qualitatively similar to a phylogeny based on molecular divergence. The role of ecology in these radiations is difficult to test because their phylogeny is limited to the genus level. It is much easier to test the role of ecology in adaptive radiations at the lowest taxonomic levels. Aside from these studies, the majority of research relevant to the adaptive radiation of dabbling ducks has progressed largely independently within the three fields.

1.4.1 Common Ancestry and Genetic Determination

The first two criteria, common ancestry and genetic basis of phenotypic traits, are easily satisfied. Dabbling ducks within the genus *Anas*, when combined with four other species of South American ducks, form a monophyletic clade, although Mallards (*A. platyrhynchos*) appear to be polyphyletic (Johnson and Sorenson 1999). All of the studies in the following discussion are of sympatric species, indicating variation in morphology has a genetic basis.

1.4.2 Evidence of Divergent Selection Between Environments

Both bill morphology and body length have been proposed as phenotypic traits that play a key role in the ecological diversification of dabbling ducks. I summarize the evidence for divergent selection between environments on these two traits separately.

Dabbling ducks filter prey from water using lamellae located on the bill (Kooloos et al. 1989; Zweers et al. 1977). Ducks with high lamellar density (lamellae cm^{-1}) are thought to have small spaces between their lamellae allowing them to retain small prey, while species with low lamellar density have large spaces and can retain only large prey (Crome 1985; Kooloos et al. 1989; Mott 1994), possibly leading to size-based resource partitioning (Nudds and Bowlby 1984; Nummi 1993; but see Nummi et al. 1995; Nummi and Väänänen 2001).

The logical argument for divergent selection on lamellar density between environments is not strong because the interaction between lamellar density and prey size alone does not propose a trade-off in foraging performance (Bethke and Nudds unpublished). Species with high lamellar density, such as Northern Shovelers (*A. clypeata*), can forage on large and small invertebrates, while species with low lamellar density, such as Mallards (*A. platyrhynchos*), can feed only on large invertebrates. What is the advantage of having large lamellar spacing? Indeed, Shovelers had higher ingestion rates than Mallards regardless of prey size (Mott 1994). Similarly, Kooloos

et al. (1989) reported that Shovelers had higher ingestion rates than Mallards when foraging on small prey, but the pattern was reversed when foraging on large prey. However, the decline in intake rate of large prey by Shovelers was due to a decline in water filtration rate. Both species retained almost all the large prey that entered their bills.

Lamellar density does not fair well in field tests either. Some studies have predicted a positive correlation between lamellar density and the depth of the water in which species feed because shallow water contains larger invertebrates than deeper water (Armstrong and Nudds 1985; Mittlebach 1981; Nudds 1992), but these correlations are rarely statistically significant (Nudds et al. 2000; Nudds et al. 1994; Pöysä et al. 1996).

In response to these difficulties, it has been suggested that detritus (e.g., sand, silt and dead vegetation), imposes a foraging cost (Bethke and Nudds unpublished; Tolkamp 1993). If large prey occurred with high concentrations of small detritus, but small prey occurred with no detritus, then a foraging trade-off may result. Species with high lamellar density foraging on large prey would also retain detritus, while species with low lamellar density would retain only prey. When foraging on small prey, species with high lamellar density would be able to retain prey, but species with low lamellar density would not. The assumed correlation between prey and detritus size is plausible. Within the range of foraging depths accessible to ducks, shallow water should contain more detritus than deeper water.

Tests of this idea have produced mixed results. Detritus does cause a decline in prey ingestion rates of ducks (Guillemain et al. 1999; Tolkamp 1993; Van Eerden 1997), and Shoveler intake rates did decline more than species with low lamellar density, but there is no evidence this trade-off predicts divergence in phenotypes. When detritus was present, Shoveler ingestion rates were greater than, or equal to, the ingestion rates of the other species (Tolkamp 1993). Contrary to expectations, the ducks did not ingest any detritus, even though it was larger than their lamellar spacing. The test allowed ducks to forage on only one size-frequency distribution of prey and detritus, so other distributions may allow Mallards to achieve greater filtration rates than Shovelers.

The ability of Shovelers to avoid ingesting detritus suggests lamellar spacing alone does not determine the minimum size of particles ingested. Detailed studies of bill biomechanics show elevation and depression of the maxilla and mandible allow the distance between the maxillary and mandibular lamellae to be greater than the interlamellar distance (Kooloos et al. 1989). Adjustment of bill position might allow ducks some ability to avoid ingesting small particles. This would explain Tolkamp's (1993) results because he fed ducks prey that were

larger than the detritus particles. The decline in filtering rates Tolkamp observed may be due to biomechanical trade-offs related to movement of the maxilla and mandible, which may reduce the rate at which water is pumped through the bill (Crome 1985; Kooloos et al. 1989). Further study is needed to integrate the biomechanics of filter-feeding with variation in environmental conditions.

A clear trade-off has been demonstrated between foraging modes used by ducks. In addition to filtering prey, ducks can ingest prey by pecking. The choice of mode is determined by the presence of water and by prey size. Ingesting rate while filter-feeding declines with increasing prey size, while intake rate while pecking increases with prey size (Kooloos and Zweers 1991). Mallards achieve equal prey intake rates using the two modes when prey are 6.5 mm in diameter (Kooloos and Zweers 1991). The biomechanics of the two modes conflict and could lead to divergent selection on many aspects of bill and tongue morphology and function (Kooloos and Zweers 1991). Filter-feeding ducks should have large bills to increase filtration rate and tongues specialized for pumping. They should also transport food to the esophagus under the tongue. This is necessary because the tongue is held against the roof of the maxilla to avoid swallowing water while filter-feeding. Pecking ducks should have short bills, simplified tongues and should transport food to the esophagus over the tongue. Foraging trials between Mallards, Wigeon (*A. penelope*) and White-fronted Geese (*Anser albifrons*) confirm the predicted trade-off: Mallards have higher intake rates than Wigeon when filter-feeding, while the opposite is true while grazing (Van Der Leeuw et al. 2003). Wigeon represent an intermediate phenotype between the pecking and filter-feeding extremes. They transport food under the tongue while geese, which graze predominately, transport food over the tongue. The filter-feeding performance of geese is much poorer than Mallards or Wigeon.

Although the functional trade-off between grazing and filter-feeding is evidence of divergent selection between environments, it isn't clear how much diversity it can explain. At its most basic, the trade-off may only favour two groups of filter-feeding and grazing specialists. Are there environments in which the performance of species with intermediate phenotypes is paramount? Current knowledge suggests intermediate phenotypes would perform best obtaining relatively large prey items from aquatic environments. The potential for the grazing-filtering trade-off to explain the larger radiation of ducks and geese warrants more study.

Dabbling ducks are poor divers and invert themselves (i.e. tip-up) to reach food below the surface. Interspecific differences in body length constrains how deep each species can forage, leading to vertical partitioning of resources (Pöysä 1983a; Pöysä 1983b; Pöysä et al. 1994).

However, body length alone fails to provide a trade-off leading to divergent selection between environments. Because large ducks can forage everywhere small ducks can, there is no apparent advantage to being a small duck.

Variation in body size imposes ecological trade-offs through other mechanisms (Peters 1983). For example, animals with small bodies have lower metabolic energy costs, but higher mass-specific metabolic rates, than larger animals. Consequently, small waterfowl are able to meet their energy requirements at lower food density than large waterfowl (Sutherland and Allport 1994), but require higher quality food than large waterfowl (Bruinzeel et al. 1997). This trade-off is caused by limitations on digestibility of food as much as energetic demand. To compensate for the decline in food quality, birds increase gut volume (Karasov 1996), which is limited by body size.

Although digestion imposes constraints on energetic gain, differences in gut morphology and function between species have received little attention. Variation in gut morphology of waterfowl is correlated with diet (Barnes and Thomas 1987), but only weakly with bill morphology (Kehoe and Thomas 1987), suggesting two independent phenotypic traits. The morphology of avian digestive systems is relatively plastic and responds quickly to changes in diet (Karasov 1996), so high variability is expected. In spite of this plasticity, trade-offs between diet and digestive performance have been demonstrated in other birds (Karasov and Levey 1990; Witmer and Van Soest 1998).

1.4.3 Evidence of Divergent Selection Due to Negative Interspecific Interactions

Three studies have attempted to test for patterns of divergent character displacement in ducks. Pöysä et al. (1994) and Osnas and Ankney (2003) tested for evidence of over-dispersion of lamellar density and body length by analysing the distribution of dabbling ducks among wetlands. Both studies compared their results to expectations from null models. Neither study found any difference between the expected and observed distributions for lamellar density, while body length was either over-dispersed (Pöysä et al. 1994) or under-dispersed (Osnas and Ankney 2003). Pöysä et al. (1994) also showed that the dispersion of body length increased as the abundance of invertebrates in the wetlands declined, while the dispersion of lamellar density was not correlated with invertebrate abundance or with prey size diversity. However, it isn't evident that dispersion should increase under these conditions. If lamellar density constrains the size of prey that can be consumed, a decrease in prey size diversity would restrict the ducks using these wetlands to those with similar lamellar density. Nudds and Wickett (1994) found that species

with a body mass ratio less than the average of 1.2 co-occurred less often than expected by chance on the breeding grounds. Patterns of co-occurrence did not differ from the null expectation on the wintering grounds. They concluded that interspecific interactions are more likely to influence community assembly on the breeding grounds.

These three studies easily satisfy three of the required criteria. The first and fifth criteria are satisfied because the species are sympatric and all three studies utilized null models, satisfying the second criterion.

To satisfy the third criterion, evolutionary shifts in phenotype would have to be inferred from a phylogeny. I am unaware of any study that has mapped body size or lamellar density of species onto an independent phylogeny. The alternative hypothesis is species sorting, which occurs when species are lost from communities through extinction. Species sorting is a plausible mechanism for communities of Holarctic dabbling ducks. The phylogeny of *Anas* is not congruent with geographical distribution and communities of sympatric species may not include close relatives (Johnson and Sorenson 1999). The geographic origins of some species are not clear, but only two lineages commonly studied in the Holarctic are thought to have diverged in the northern hemisphere (Johnson and Sorenson 1999). Holarctic communities may have been shaped primarily by differences in species' ability to colonize and persist in the northern hemisphere.

The fourth criterion requires that differences in resource use are linked to differences in phenotype. Guillemain et al. (2002) provide the best evidence of a link between body length and resource use. At the start of the winter they observed that small Green-winged Teal and large Mallards forage in shallow water on large seeds. Over the course of the winter, Mallards continued to forage on large seeds, but switched to foraging in deeper water while Teal continued to feed in shallow water, but switched to feeding on small seeds. The authors attributed the change in foraging habitat and seed size to depletion of seeds, although they did not measure seed abundance over time. However, they argued that Mallards switch to deeper water before Teal because Mallards have low lamellar density, which reduces their ability to forage on small seeds compared to Teal. Other studies have not shown such clear differences in resource use. Pöysä (1986) compared the depths at which different species foraged alone and in the presence of other species. Foraging depths diverged when foraging in the presence of other species in only three of 12 comparisons.

Evidence from the field linking differences in lamellar density with differences in resource use is lacking. A number of studies have compared the size-frequency distribution of

prey ingested by different duck species (Guillemain et al. 2002; Nudds and Bowlby 1984; Nummi 1993; Nummi et al. 1995; Nummi and Väänänen 2001), but these studies can not be used to test for a correlation between lamellar density and prey size. All four studies assigned prey to size categories such that all but one were larger than the lamellar spacing of any duck.

Criteria six requires independent evidence that species compete. The majority of this evidence is indirect. Interspecific aggression among waterfowl is frequent (Anderson and Titman 1992; Connelly and Ball 1984; Eddleman et al. 1985; Joyner 1977; Ryder 1959; Savard 1982; Savard and Smith 1986; Thompson and Baldassarre 1992), often associated with kleptoparasitism (Bailey and Batt 1974; LeSchack and Hepp 1995; Ryan 1980) and may lead to death (Eadie and Lyon 1998; Livezey and Humphrey 1985; Nuechterlein and Storer 1985a; Savard 1987). A number of these authors have suggested aggression is related to resource defense. Competition can result if resources decline in abundance, either due to consumption by ducks or other factors. The abundance of both summer food (invertebrates) (Armstrong and Nudds 1985; Mittlebach 1981; Nudds 1992) and winter food (seeds and invertebrates) (DuBowy 1988; Guillemain et al. 2002) decline seasonally, although variation in niche overlap suggests competition is more likely in winter than summer (DuBowy, 1988; but see Bethke, 1991).

There is only one experimental test of competition among species of dabbling ducks. Elmberg et al. (1997) stocked 32 lakes with wing-clipped Mallards before the arrival of Green-winged Teal (*Anas crecca*) in the spring. Mallard density was 2.9 to 8 times greater than the pre-treatment levels. The following year the control and treatment lakes were reversed. Elmberg et al. concluded Mallards and Teal do not compete because they found no difference in the number of Teal using lakes with and without captive Mallards. This conclusion should be treated with caution because presence/absence is a coarse measure of fitness. Increased density of Mallards may have reduced Teal fitness, but not enough to cause Teal to select a different lake. If the variation in fitness between lakes is great (as the authors indicate), Teal may be willing to accept a large decline in fitness caused by competition before they switch to another lake. Unfortunately, the authors do not report if the presence of captive Mallards affected the presence of wild Mallards. If not, it is difficult to accept their conclusion because interspecific competition should be stronger than intraspecific competition. Regardless, because this experiment dealt with only two species, it falls short of demonstrating competition is negatively correlated with differences in phenotype.

1.4.4 Ecological Speciation

Waterfowl are well known for their propensity to hybridize (Grant and Grant 1992; Johnsgard 1960). If interspecific variation in hybridization frequency is high, waterfowl may be a good taxa to test for evidence of ecological speciation. On the other hand, high frequencies of hybridization over-all may suggest little ecological divergence. Tests for a relationship between the two have not been conducted because a comprehensive method to quantify ecological divergence between species is lacking. Despite this gap, some information exists about the relationship between hybridization frequency and relatedness. Tubaro and Lijtmaer (2002) compared 161 interspecific crosses totalling 1037 hybrids to a randomly generated distribution of crosses and found a surplus of hybrid crosses among closely related species and a scarcity among distantly related species. However, after controlling for relatedness, reproductive isolation was stronger among allopatric species compared to sympatric species. The authors noted that the frequency of crosses between allopatric species might be low because of a lack of opportunity for hybridization rather than the presence of barriers to hybridization.

1.5 Synthesis and Prospectus

The evidence for adaptive radiation of dabbling ducks, and waterfowl in general, ranges from weak to absent. This is not surprising given that evolutionary ecologists have rarely considered waterfowl in the context of adaptive radiation. Even many of the celebrated radiations still lack strong evidence of one or more processes and much of the evidence in support of the ecological theory of adaptive radiation in general is recent (Schluter 2000).

The evidence that does exist leads to an interesting dichotomy. The evidence for divergent selection between environments provides more support for bill morphology as a key trait involved in the ecological diversification of dabbling ducks, while the evidence for divergent selection between competitors supports body length. Of the two traits, body length seems the least plausible. The failure to identify a performance trade-off due to body length is a serious weakness. In comparison, lack of evidence of over-dispersion of lamellar density (Osnas and Ankney 2003; Pöysä et al. 1994) may be due to type II error. Resource use may be determined by a complex interaction between lamellar density and other morphological traits, or resource partitioning may exploit variation within ponds more than variation between ponds. Alternatively, these results might be considered complementary because both traits deal with resource acquisition. Body length and lamellar density are negatively correlated across species,

suggesting they are co-evolved. Obviously, much work will be necessary to resolve these uncertainties.

Future studies may best be directed at elucidating the phenotypic basis of ecological differences between species. Given this knowledge, predictions regarding the relationship between phenotypic differences, competitive interactions and barriers to reproduction could be tested. Because of their large body size, migratory behaviour and large population sizes, approaches based entirely on experimentation or direct measures of fitness in the wild will be difficult. Instead, experimentation may best be directed at particular traits to gain a mechanistic understanding of how phenotypes interact with environmental variation to determine resource use (Moermond 1986; Schoener 1986; Wainwright 1996; Werner 1984). These results could then be used to make quantitative predictions about competitive interactions and reproductive isolation that are tested by observational and experimental field studies.

1.6 Thesis Outline

I pursued this strategy in completing this thesis. I integrated bill biomechanics with environmental conditions typically encountered by filter-feeding ducks to gain predictive insight into the constraints morphology imposes on resource use. To begin, I conducted a simple experiment that tested whether filter-feeding ducks can avoid ingesting detritus by adjusting the position of the maxilla and mandible to expel small particles (Chapter 2). I then modelled the biomechanics of filter-feeding to predict prey intake rates of two species of dabbling ducks. I tested these models using experimental data reported in the literature to show there is a trade-off between filtration rate and detritus avoidance that is influenced by bill morphology (Chapter 3). I then constructed foraging models for seven species of dabbling ducks to test whether the trade-off between filtration rate and detritus avoidance leads to interspecific resource partitioning. I simulated different size-frequency distributions of prey and detritus and predicted net energetic rates of each species. As prey density declined, the models predicted species would begin to exploit different sized prey due to the trade-off between filtration rate and detritus avoidance (Chapter 4). To determine if phenotypic divergence is the result of negative interspecific interactions, I tested for a negative correlation between frequencies of interspecific aggression and phenotypic divergence. As predicted, niche separation estimated from the foraging models was negatively correlated with frequencies of aggressive interactions between species measured in the field (Chapter 5). Finally, in Chapter 6, I summarize these findings in the context of evidence for adaptive radiation in waterfowl, identify remaining knowledge gaps and suggest

how the results of this thesis can be built upon to fill these gaps. I comment also on the application of my findings to current issues concerning the conservation of dabbling ducks.

CHAPTER 2

FILTER-FEEDING DABBING DUCKS (*ANAS*) CAN SELECT PARTICLES BY SIZE

2.1 Abstract

Interspecific differences in bill morphology among sympatric dabbling ducks (*Anas*) are thought to cause partitioning of prey and thus reduce competition. However, the relationship between phenotype and resource use among filter-feeding dabbling ducks is not clear. The lamellar density hypothesis proposes that ducks with high lamellar density are more effective at filtering small particles than species with low lamellar density, possibly leading to size-based prey partitioning. The lamellar separation hypothesis proposes that the distance between the maxillary and mandibular lamellae determines the size of particles retained by ducks. Elevation and depression of the maxilla and mandible during foraging may allow ducks to adjust lamellar separation and select the size of particles that are ingested, in contrast to the lamellar density hypothesis. Both Northern Shovelers (*A. clypeata*) and Mallards (*A. platyrhynchos*) can ingest large and small seeds, but prefer large seeds. When large and small seeds were mixed together, ducks ingested more large seeds than small seeds. Small seeds were larger than the ducks' inter-lamellar distance, clearly rejecting the lamellar density hypothesis. Ducks appear to adjust the position of the maxilla and mandible to avoid retaining less preferred particles.

2.2 Introduction

Interspecific differences in phenotype are thought to reduce competition by allowing resources to be partitioned between species (MacArthur and Levins 1967; Roughgarden 1972; Slatkin 1980; Taper and Case 1992). Although phenotypic differences between species are often obvious, the relationship between phenotype, function and resource use under different environmental conditions is rarely quantified (Wainwright 1991; Wake 1992), leaving the adaptive value of the phenotypic trait open to question.

Lack (1971; 1974) suggested that differences in bill morphology among sympatric dabbling ducks may lead to food partitioning, but the functional relationship between foraging efficiency and morphology is not yet clear. When filter-feeding, ducks use lingual movements to create a one-way flow of water from the anterior of the bill to the posterior (Zweers et al. 1977). At the posterior, lateral margins of the bill, comb-like structures (lamellae) filter food particles from the flow of water exiting the bill (Kooloos et al. 1989; Zweers et al. 1977). Ducks with high lamellar density (lamellae cm^{-1}) have small spaces between their lamellae (small inter-lamellar distance) and are more effective at filtering small particles than species with low lamellar density (Crome 1985; Kooloos et al. 1989; Mott 1994), possibly leading to size-based resource partitioning (Nudds and Bowlby 1984; Nummi 1993; but see Nummi et al. 1995; Nummi and Väänänen 2001). However, variation in inter-lamellar distance alone cannot lead to resource partitioning because it does not provide an interspecific trade-off in foraging performance: species with high lamellar density ingest prey at greater rates regardless of prey size (Mott 1994).

Bethke and Nudds (unpublished) noted that ducks frequently encounter particles with low nutritional value (detritus) while foraging and suggested that detritus may occlude the lamellae and reduce water flow through the bill. They thought greater inter-lamellar spacing may reduce occlusion, but at the expense of reduced prey capture, possibly providing the performance trade-off necessary for interspecific partitioning of resources. Detritus does reduce the ingestion rates of feeding ducks (Tolkamp 1993; Van Eerden and Munsterman 1997). Tolkamp (1993) observed that detritus caused a greater reduction in the filtration rates of ducks with high lamellar density compared to species with low lamellar density, but the reduction was not correlated with inter-lamellar spacing and ducks with greater lamellar density still had the highest filtration rates when foraging in the presence of detritus. Tolkamp also found that ducks did not ingest detritus, even when the detritus particles appeared to be larger than the ducks' inter-lamellar distance.

Kooloos et al. (1989) and Crome (1985) suggested the size of particles retained by foraging ducks may be determined by the distance between lamellae on the maxilla and mandible (lamellar separation) rather than solely by inter-lamellar distance. Elevation and depression of the maxilla and mandible while foraging may allow ducks to adjust lamellar separation and select the size of particles that are ingested (Crome 1985; Kooloos et al. 1989; Zweers and Vanden Berge 1997), but this ability has not been tested. Such an adjustable filter would weaken the functional relationship between inter-lamellar distance and prey size. The lamellar separation hypothesis could explain Tolkamp's (1993) observation that ducks were able to filter prey while avoiding detritus, but this explanation assumes that the ducks were capable of ingesting the detritus particles. Tolkamp used dead leaves as detritus, which are very thin, and may have passed between the lamellae.

I conducted a series of foraging trials with captive dabbling ducks to test between the lamellar density and lamellar separation hypotheses. I used variation in preferences for seeds of different sizes to test if dabbling ducks can actively select the size of particles they ingest while filter-feeding.

2.3 Methods

Foraging trials were conducted with a male and female Mallard (*A. platyrhynchos*) and a single female Northern Shoveler (*A. clypeata*) obtained from Delta Waterfowl Trust, Portage la Prairie, Manitoba. The ducks were hatched in captivity from eggs laid by wild ducks and were at least 2 years of age. These two species have the most divergent inter-lamellar distance (Kooloos et al. 1989; Nudds and Bowlby 1984) and lamellar length (Kooloos et al. 1989) of Holarctic *Anas*. Filtration of particles 0.5-1.2 mm in diameter is achieved almost entirely by the dorsal mandibular lamellae (Kooloos et al. 1989). Over the region of the bill where filtration occurs, the inter-lamellar distance of the dorsal mandibular lamellae of Shovelers varies between 0.3 and 0.4 mm, while Mallard inter-lamellar distance varies between 0.6 and 0.7 mm (Kooloos et al. 1989).

Prior to the experiment, I presented the ducks with a variety of commercially available seeds to determine if they preferred to consume some types over others. I found they readily consumed wheat and millet, but would not consume poppy seeds until they went without other food for 24 hours. Poppy seeds, millet and wheat sieved into three, non-overlapping size classes: 0.5-1.0 mm, 1.4-2.0 mm, and 2.8-4 mm, respectively. Direct measurements revealed only eight percent of poppy seeds were smaller than 0.6 mm. Poppy and millet seeds were round while wheat seeds were oval. If inter-lamellar distance determines the size of the particles retained,

then ducks should consume seeds larger than the inter-lamellar distance in equal proportion to their availability.

Alternatively, if lamellar separation determines particle retention, ducks should consume more millet and wheat than poppy seeds. In addition to affecting particle retention, elevation and depression of the maxilla and mandible forces water out of the bill (Kooloos et al. 1989; Zweers et al. 1977). Because the pumping action causes lamellar separation to vary, small seeds may always have lower retention rates than large seeds. Consequently, acceptance of the lamellar separation hypothesis does not necessarily infer ducks actively avoided ingesting poppy seeds. I tested for evidence of active selection by comparing my data to other measurements of filter-feeding performance reported in the literature. Mott (1994) measured the slope of the functional response (i.e. the change in prey intake rate with change in prey density) for Mallards and Shovelers feeding on daphnia 0.8-1.0 mm long and 1.2-1.4 mm long. The slopes for Mallards were 0.24 and 0.30, respectively, and for Shovelers they were 0.46 and 0.50, respectively, although the slopes did not differ statistically when compared within species. Kooloos et al. (1989) found that Mallards retained 67% of poppy seeds (0.7-1.2 mm) and 95% of millet seeds (1.2-2.4 mm) that entered their bill, while Shovelers retained 95% of poppy seeds and 93% of millet seeds. Retention of the two seed types by Shovelers did not differ statistically. If ducks are unable to forage selectively, Mott's measurements predict the ratio of seeds (millet/poppy) consumed by Mallards and Shovelers should be 1.25 and 1.09, respectively. Kooloos et al.'s measurements predict the ratio of seeds consumed by Mallards and Shovelers should be 1.42 and 0.98, respectively. If ducks actively avoid ingesting poppy seeds, then they should ingest fewer poppy seeds than millet seeds, and the observed ratio of seeds ingested should be greater than the expected ratio.

Foraging trials were conducted between April and June 2001. During the trials the ducks were held in separate, outdoor pens at the Animal Care Facility at Simon Fraser University where they had continuous access to water for drinking and bathing. When not engaged in foraging trials, ducks were fed a standard mixture of two parts commercial poultry feed, one part wheat and a small amount of commercial grit and oyster shell. Regular allotments (125 ml for Mallards; 63 ml for the Shoveler) of the standard mixture were mixed in 1.5 L of water and given to the ducks at 08:00 PST daily. Any remaining food was removed by 16:00 the same day. Earlier work indicated this feeding schedule kept the ducks at a constant body mass while ensuring they would feed readily each morning.

A mixture of 10 g (dry weight) each of wheat, millet, and poppy seeds were presented ten times to each duck. The foraging performance of each duck was measured at two different times. All trials adhered to the following schedule. At 08:00 on day one, the dry seed mixture was combined with 0.5 L of water to ensure all seeds sank. Wet mixtures were combined with 1 L of water and placed in bowls in each duck's pen. Bowls were fixed in a circular hole in a wooden platform to ensure the bowl could not tip over and seeds splashed out of the bowl could be collected. After 1 hour, trial mixture A was removed and replaced with a regular food allotment. The uneaten seeds of trial A were filtered from the water, left to dry for 20 hours, then sieved, weighed to the nearest 0.01 g and remixed. The mass of seeds was adjusted to account for residual water absorption. These steps were repeated on day two with a new trial mixture (B), except that following removal of trial B, the ducks were given the remaining seeds from trial A, rather than their food allotment, and left for 23 h. On day three the remaining seeds from trial A were removed, replaced with the uneaten seeds from trial B, and left overnight. Remaining trial A seeds were filtered, dried, sieved and weighed. On day four trial B seeds were removed and replaced with a regular food allotment. Remaining trial B seeds were filtered, dried, sieved and weighed. On days five, six and seven no trials were conducted and ducks received their regular food allotment. The schedule was repeated again on day eight. Trace amounts of seeds were recorded as 0.01 g.

2.4 Results

The amount of seed consumed by the ducks depended on seed size, foraging period and the interaction between these two factors (Table 2.1; Fig. 2.1). During the first foraging period, all three ducks filtered more millet and wheat seeds than poppy seeds (independent contrasts poppy vs. others: female shoveler $F_{1,27}=1862.85.16$, $P<0.0001$; female mallard $F_{1,27}=1983.98$, $P<0.0001$; male mallard $F_{1,27}=1603.05$, $P<0.0001$). In fact, there were never any wheat seeds remaining after the first foraging period. All three ducks consumed fewer poppy seeds during the first foraging period than the second (independent contrasts poppy 1 vs. poppy 2: female shoveler $F_{1,18}=1618.26$, $P<0.0001$; female mallard $F_{1,18}=1011.05$, $P<0.0001$; male mallard $F_{1,18}=364.09$, $P<0.0001$). The female ducks always consumed more poppy seeds than the male duck by the end of the second foraging period. The ducks consumed more millet than poppy seeds during the first foraging period (Table 2.2). The proportions of large seeds consumed by all three ducks were significantly greater than the proportion expected if ducks were not selective.

2.5 Discussion

The foraging performance of the ducks rejects the lamellar density hypothesis and is consistent with the lamellar separation hypothesis. If inter-lamellar distance limited the minimum size of particles that could be avoided, the ducks should not be able to avoid consuming poppy seeds because the poppy seeds are larger than their inter-lamellar distance. However, the ducks did avoid filtering most of the poppy seeds during the first foraging period. The difference in the amount of millet and poppy seeds consumed was not due to inherent differences in their ability to consume the two types of seeds. The ducks ingested fewer poppy seeds than expected when foraging on poppy seeds alone, indicating they actively avoided poppy seeds.

It is unlikely the ducks ingested more millet seeds than expected. Observations of the ducks during the first foraging period confirmed that they were filter-feeding and not selecting individual seeds by pecking. The ducks fed rapidly and were frequently finished feeding in less than 1 minute. Because poppy seeds are lighter than millet and wheat seeds, all three seed types must have entered the ducks' bills. To avoid consuming the poppy seeds, it is most likely the ducks elevated their maxilla or depressed their mandible to increase lamellar separation and allow the poppy seeds to exit the bill while retaining the millet and wheat. Shovelers and Mallards can achieve lamellar separation values between 0 and 4 mm and between 0.5 and 6 mm, respectively (Kooloos et al. 1989), which would allow them to separate the poppy seeds from the millet and wheat seeds. Kooloos et al. observed that particle retention, including retention of poppy seeds, decreased when lamellar separation was large compared to the size of the food particles. They also observed that the ducks decreased lamellar separation while feeding to increase the retention of small food particles.

Inter-lamellar distance is less of a constraint on filter-feeding performance by dabbling ducks than lamellar separation. At most, inter-lamellar distance sets the minimum size of particles that can be retained, but not expelled. How lamellar separation sets this lower constraint is not well understood. Ducks can filter particles smaller than the inter-lamellar distance (Crome 1985; Kooloos et al. 1989; Mott 1994), perhaps by inertial deposition rather than sieving (Kooloos et al. 1989). It is not known if increased lamellar separation reduces ingestion of very small particles retained by inertial deposition.

Although my observations were limited to a few individuals, I expect most species of *Anas* are capable of some degree of size selection. The kinetic skull possessed by all *Anas*, indeed all birds, allows them to move the mandible and maxilla relative to the brain case (Bout and Zweers 2001).

The ability to select particles has obvious advantages for filter-feeders that must forage from a mixture of prey and detritus particles (Guillemain et al. 1999). By adjusting lamellar separation, ducks could expel particles that provide low nutritional return. Large particles could be excluded by reducing the separation between the maxilla and mandible at the bill tip, as suggested by Van Eerden and Munsterman (1997). Flamingos (*Phoenicopterus ruber*) are capable of selecting particles by exclusion and expulsion (Zweers et al. 1995). Ducks are capable of rapidly discriminating between prey and detritus using the bill tip organ (Wouterlood and Zweers 1973), enabling them to make appropriate adjustments to bill position.

The lamellar separation hypothesis provides an explanation for interspecific differences in the reduction of filtration rates caused by avoiding detritus. Tolkamp (1993) observed that foraging in the presence of detritus caused the filtration rates of Shovelers to decline by 50% while rates of Mallards and Blue-winged Teal (*Anas discors*) declined by only 27% and 9%, respectively. Kooloos et al. (1989) found that depression of the maxilla and mandible, which is necessary to increase lamellar separation, caused a decline in the lingual stroke volume. Since Shovelers have longer lamellae than Mallards (Kooloos et al. 1989) and Blue-winged Teal (pers. obs.), Shovelers must depress their maxilla and mandible more to achieve the same lamellar separation. Shovelers should, therefore, experience a greater decline in their filtration rates as a result of reduced lingual stroke volume. This morphology-performance trade-off may lead to inter-specific resource partitioning. Quantifying the trade-off between particle size selection and changes in lingual stroke volume may provide predictive insight into the foraging ecology of dabbling ducks.

Table 2-1 Results of analysis of variance on mass of three types of seed remaining after foraging by three individuals of two species of dabbling ducks (*Anas spp.*). Seed remaining was measured 1 hour and 24 hours after seed was made available to the ducks.

Species	Sex	Source	df	SS	MS	F	P
<i>A. clypeata</i>	F	Seed	2	219.42	109.71	944.03	<0.0001
		Time	1	136.99	136.99	1178.77	<0.0001
		Seed*time	2	215.34	107.67	926.48	<0.0001
		Error	54	6.28	0.12		
		Total	59	578.01			
<i>A. platyrhynchos</i>	F	Seed	2	237.78	118.89	1003.68	<0.0001
		Time	1	123.5	123.5	1042.58	<0.0001
		Seed*time	2	232.07	116.03	979.58	<0.0001
		Error	54	6.39	0.12		
		Total	59	599.74			
<i>A. platyrhynchos</i>	M	Seed	2	396.9	198.45	854.38	<0.0001
		Time	1	116.07	116.07	499.69	<0.0001
		Seed*time	2	84.07	42.03	180.96	<0.0001
		Error	54	12.54	0.23		
		Total	59	609.57			

Table 2-2 Results of paired *t*-tests for selective consumption of millet and poppy seeds by three dabbling ducks (*Anas spp.*) after the first foraging period. Statistical tests infer the consistency of patterns within individuals because experiments were repeated with each individual. (A) The difference in the amount of seed (millet-poppy) consumed. Difference (observed-expected) between the observed ratio (millet/poppy) of seed consumed when mixed and the ratio expected when seeds are not mixed based on data from (B) Mott (1994) and from (C) Kooloos et al. (1989).

Species	Sex	Mean	S.E.	<i>t</i> ₉	<i>P</i>
A					
<i>A. clypeata</i>	F	7.70	0.21	35.9	<0.0001
<i>A. platyrhynchos</i>	F	8.31	0.27	30.5	<0.0001
<i>A. platyrhynchos</i>	M	6.32	0.18	35.2	<0.0001
B					
<i>A. clypeata</i>	F	5.80	1.03	5.62	0.0003
<i>A. platyrhynchos</i>	F	7.16	1.33	5.39	0.0004
<i>A. platyrhynchos</i>	M	7.06	1.52	4.65	0.0012
C					
<i>A. clypeata</i>	F	5.91	1.03	5.73	0.0003
<i>A. platyrhynchos</i>	F	6.99	1.33	5.27	0.0005
<i>A. platyrhynchos</i>	M	6.89	1.52	4.53	0.0014

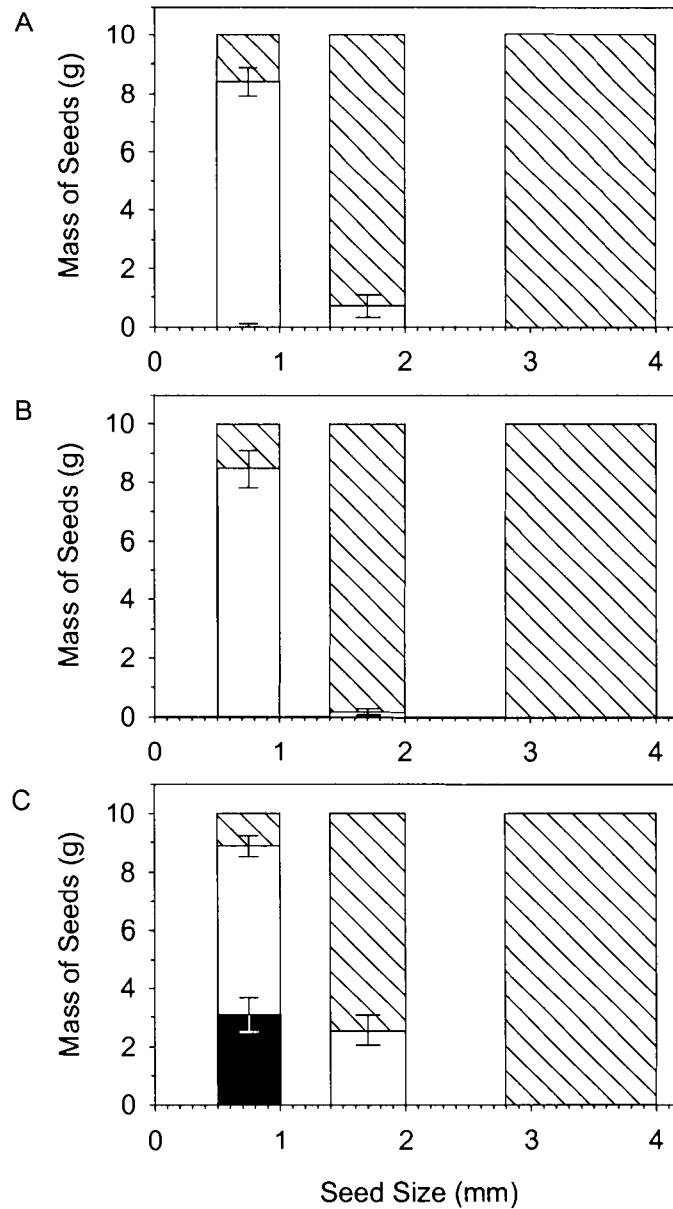


Figure 2-1 Consumption of poppy (0.5-1.0 mm), millet (1.4-2.0 mm) and wheat (2.8-4 mm) seeds by a female Northern Shoveler (A) and a female (B) and male (C) Mallard. Ducks began foraging on a mixture of 10g of each seed type. Bars indicate the mass of seed consumed during the first hour (hatched), during the following 23 hours (open), and the mass remaining after 24 hours (solid). Error bars indicate 95% confidence intervals around the mean of 10 replicates.

CHAPTER 3 PREDICTING INTERSPECIFIC VARIATION IN FORAGING RATES OF FILTER-FEEDING DABBING DUCKS FROM FUNCTIONAL MORPHOLOGY

3.1 Abstract

Interactions between phenotypes, resources and environments are thought to result in interspecific resource partitioning and are often invoked to explain variation in species' abundances between environments. Resource partitioning requires that these interactions include a performance trade-off. Variation in bill morphology is thought to lead to partitioning of prey by size among filter-feeding dabbling ducks (*Anas*), but a foraging trade-off leading to resource partitioning has not been demonstrated. I developed biomechanical models to predict the effects of prey and detritus size-frequency distributions on the foraging rate of Mallards (*A. platyrhynchos*) and Northern Shovelers (*A. clypeata*). The models correctly predicted variation in water filtration rates, particle retention probabilities and prey ingestion rates measured during foraging experiments that included modification of bill morphology. Results indicate both species filter prey via a sieving mechanism, rather than inertial deposition, as previously reported. In the absence of detritus, Shovelers have greater filtration rates and retain a wider size range of prey than Mallards. However, because of their long lamellae, Shovelers face a greater decline in filtration rates than Mallards when avoiding small detritus particles. This performance trade-off can lead to resource partitioning, but only when environments with small prey contain low concentrations of detritus (preferred by Shovelers) and environments with large prey have high concentrations of small detritus (preferred by Mallards). Both species should tend to prefer environments with low detritus concentrations or large differences in size between prey and detritus. Consequently, the models predict species can have shared habitat preferences in contrast to previous studies that have assumed dabbling ducks always have distinct habitat preferences.

3.2 Introduction

Species' abundances often vary between environments. Explanations of these patterns often invoke resource partitioning through interactions between phenotype and some component of the environment, such as availability of resource types (e.g., Schluter 1994; Schluter and Grant 1984; Werner 1984) or physical characteristics of habitats (e.g., Ehleringer and Clark 1988; Irschick and Garland 2001). Resource partitioning occurs when the interaction between phenotype and resource types or environment includes a performance trade-off, such that each species is a superior competitor under certain conditions (Taper and Case 1992). Although interspecific differences in phenotype are often obvious, a causal relationship between phenotype, environment and performance is not often demonstrated (Irschick 2002; Rubega 2000; Wainwright 1991; Wake 1992).

Species of Holarctic dabbling ducks (*Anas*) are distributed non-randomly among wetlands (Nudds and Wickett 1994; Osnas and Ankney 2003; Pöysä et al. 1994). Habitat use is thought to be related to prey partitioning through the effect of interspecific variation in bill morphology on filter-feeding performance by some authors (Lack 1971; Lack 1974; Nudds and Bowlby 1984; Nudds et al. 2000; Nudds et al. 1994; Nudds and Wickett 1994; Thomas 1982), but not others (Elmberg et al. 1993; Elmberg et al. 1994; Osnas and Ankney 2003; Pöysä et al. 1994; Pöysä et al. 1996). In spite of extensive and sophisticated studies that have linked bill form and function (Kooloos et al. 1989; Kooloos and Zweers 1991; Zweers 1974; Zweers et al. 1977) and compared species' foraging performance on different prey (Crome 1985; Kooloos et al. 1989; Mott 1994; Van Eerden and Munsterman 1997) and under different habitat conditions (Tolkamp 1993; Van Eerden and Munsterman 1997), resource partitioning due to interspecific variation in bill morphology has not been demonstrated (Chapter 1). However, these empirical studies have considered such a limited range of prey types and environmental conditions, it cannot be concluded that resource partitioning does not occur.

An alternative approach to empirical studies is to begin with a mechanistic understanding of the interaction between bill morphology, resource types, environmental conditions and foraging performance (Moermond 1986; Schoener 1986; Wainwright 1996). If the hypothesized trade-off can be identified and quantified with a biomechanical model, the foraging performance of different species can be predicted for a wide range of prey types and environmental conditions.

I integrated interspecific variation in bill morphology with an explicit biomechanical model to predict the effects of prey types and environmental variation on the foraging rate of two

species of filter-feeding dabbling ducks. The models incorporated different filtering mechanisms to resolve how morphology influences prey retention. I tested these models using performance data reported in the literature by experimental foraging studies. I compared the foraging performance of the two species predicted by the models to determine if, and under what conditions, interspecific differences in morphology might lead to resource partitioning.

3.2.1 Waterfowl Ecomorphology and Filter-feeding Biomechanics

The maxilla and mandible of the anatid foraging apparatus forms a tube-like oral cavity. Dabbling ducks filter-feed by creating a flow of food and water that enters the oral cavity through the gape and is expelled laterally between the maxilla and mandible at the caudal end of the cavity (Kooloos et al. 1989; Zweers 1974; Zweers et al. 1977). Particles that pass through the gape, but not between the maxilla and mandible, are retained in the bill and ingested (Kooloos et al. 1989; Zweers et al. 1977).

Filtration is accomplished through a cycle of movements (Fig. 3.1) that utilize two mechanisms to generate a flow of water through the bill (Kooloos et al. 1989; Zweers et al. 1977). The rostral end of the tongue is thickened (lingual bulges) and, at the start of a filtration cycle, is elevated and held against the ventral side of the maxilla. In this position the lingual bulges divide the oral cavity into anterior and posterior sections. Elevation of the mandible, depression of the maxilla and retraction of the tongue caudally reduces the volume of the posterior cavity, forcing water out the lateral openings. At the end of the cycle the movements are reversed. The lingual bulges are depressed, the tongue protracts and the maxilla and mandible return to their starting position. During the reversal phase, water and food are drawn into the oral cavity through the gape. The change in volume of the posterior cavity from the start to the end of one filtration cycle determines the cycle volume. Fast, repeated cycles of these movements allow large volumes of water to be filtered quickly.

Lamellae line the lateral edges of the maxilla and mandible (Fig. 3.2) and are involved in retaining particles (Crome 1985; Kooloos et al. 1989), but different retention mechanisms have been proposed. Sieving (Rubenstein and Koehl 1977) retains particles that are too large to pass by the lamellae. Particles may pass between adjacent maxillary lamellae if they are smaller than the inter-lamellar distance (Crome 1985; Mott 1994; Nudds and Bowlby 1984; Thomas 1982) or between lamellae on the maxilla and mandible (lamellar separation, referred to as mesh size by Kooloos et al. 1989). The role of mandibular inter-lamellar distance in determining pore size has received much less attention (but see Crome 1985). While inter-lamellar distance is fixed, ducks

are capable of adjusting both gape and lamellar separation by elevation and depression of the maxilla and mandible (Crome 1985; Kooloos et al. 1989; Zweers 1974; Zweers et al. 1977), providing the ducks with some ability to select the size of particles ingested (Chapter 2). An adjustable filter would allow ducks to consume prey while avoiding indigestible detritus such as silt, sand and dead vegetation (Guillemain et al. 1999; Tolkamp 1993; Trost 1981; Van Eerden and Munsterman 1997). However, Kooloos et al. (1989) observed that surgically shortening either the mandibular or the maxillary lamellae had no effect on prey retention rates of Mallards or Tufted Ducks (*A. fuligula*). They proposed that these species retain particles by inertial impaction (Rubenstein and Koehl 1977), caused by the centrifugal force of vortices created as water passes between the maxillary lamellae.

Adjusting lamellar separation to avoid detritus is expected to produce a performance trade-off because of the dependence between cycle volume, gape and lamellar separation (Chrome, 1985; Kooloos et al. 1989; Chapter 2). To avoid detritus, gape must be reduced, or lamellar separation increased, or both. Ingesting a smaller range of particle sizes (i.e. increased selectivity) should result in lowered cycle volume and reduced water filtration rates (Fig. 3.2), but a higher concentration of energy in the ingesta. The severity of the trade-off should depend on lamellar length, because longer lamellae require greater depression of the maxilla and mandible to attain the same lamellar separation.

3.3 Methods

3.3.1 The Model

The particle ingestion rate (I) of a filter-feeding organism with a fixed pore size sieving homogenous particles can be estimated by

$$I = CVZR \tag{1}$$

where C is the concentration of particles in the environment, V is the volume of water filtered per cycle, Z is the cycle frequency and R is the retention probability of particles. Ducks can change the starting (s) and ending position (e) of the maxilla and mandible with consequences for V . R will also vary with e , s , and particle size class $i = 1, 2, 3, \dots, z$. Incorporating these constraints into equation 1 gives

$$I = \sum_{i=1}^z C_i (V_s - V_e) ZR_{s,e,i} \tag{2}$$

Ducks should adjust the position of their maxilla and mandible while foraging to give the combination of s and e that maximizes I . See Table 3.1 for a description of all model parameters.

3.3.1.1 Cycle Volume

The cycle volume is determined by the change in volume of the posterior cavity (B) between the start and end of the filtration cycle minus the volume of the tongue (T). The region of water expulsion extends from 70% to 95% along the caudal portion of the bill (Kooloos et al. 1989), which I refer to as k and j , respectively. The cavity is defined as the interior volume of the bill between the point of contact of the lingual bulges with the ventral surface of the maxilla (n , measured from the mandible tip) to the lingual cushion (Zweers et al. 1977). The lingual cushion is a thickened region at the caudal end of the tongue which is held in contact with the ventral surface of the maxilla and seals the esophagus and trachea during filtration (Zweers et al. 1977). I assumed the rostral end of the lingual cushion contacts the maxilla at j . This is a reasonable assumption since soft tissue surrounds the tongue at j and likely creates a seal around the tongue. The volume of the tongue within the posterior cavity changes as it retracts from the start (T_s) to the end (T_e) of the cycle. Cycle volume (V) is given by

$$V = V_s - V_e = B_s - T_s - B_e - T_e \quad 3$$

The maximum separation (d) between the maxilla and mandible at which filtration can occur is the sum of the maximum elevation of the tongue (l) and the tongue's thickness when depressed (h). Kooloos et al. (1989) observed that neither l nor the distance of lingual retraction ($n_s - n_e$) varied with bill position or prey size, so I assumed Kooloos et al.'s estimates of these parameters were maximums. This assumption is justified because the foraging conditions Kooloos et al. provided the ducks favoured large cycle volumes. Note that the models allow values of l and $n_s - n_e$ to be constrained by bill position to be less than maximum.

3.3.1.2 Cycle Rate and Filtration Rate

Cycle rate (Z) is determined primarily by the rate of elevation and retraction of the tongue. Estimates of Z for Mallards varied between 20-17 cycles s^{-1} and 12-13 cycles s^{-1} for Shovelers. Kooloos et al. (1989) showed little covariation between cycle rate and prey size, so I assumed the mean values they gave were constant. Water filtration rate (F) is the product of cycle rate and cycle volume.

3.3.1.3 Retention

Particles smaller than the gape, but larger than the lamellar separation, are retained and ingested. Both lamellar separation (m_e) and gape (g_s) vary with the position of the mandible and maxilla, but they also change with distance along the mandible. To quantify the effect of distance (x ; measured from the mandible tip) on the probability ($G_{s,i}$) a particle of size i passes through the gape, but not between the lamellae ($M_{e,i}$), I assumed that $m_e = \theta_e(x) = v + wx + yx^2 + zx^3$, where $k \leq x \leq j$, and that $g_s = \Omega_s(x) = v' + w'x + y'x^2 + z'x^3$, where $0 \leq x \leq n$. Given a particle of size class i with lower boundary a and upper boundary b such that: $\Omega_s(x) \geq a$ between x_1 and x_2 ; $\Omega_s(x) \geq b$ between x_3 and x_4 ; $\theta_e(x) \leq a$ between x_5 and x_6 ; and $\theta_e(x) \leq b$ between x_7 and x_8 , then

$$G_{s,i} = \left(\int_{x_1}^{x_2} \Omega_s(x) + \int_{x_3}^{x_4} \Omega_s(x) \right) / 2 \int_0^n \Omega_s(x) \quad 4$$

$$M_{e,i} = \left(\int_{x_5}^{x_6} \theta_e(x) + \int_{x_7}^{x_8} \theta_e(x) \right) / 2 \int_k^j \theta_e(x) \quad 5$$

and

$$R_{s,e,i} = G_{s,i} M_{e,i} \quad 6$$

If particles can pass between the maxillary or mandibular lamellae, then inter-lamellar distance will determine the value of i at which $M_{e,i} = 0$. I constructed models that assumed retention was determined by three different mechanisms: lamellar separation alone (LS model); lamellar separation and maxillary inter-lamellar distance (MAX model); and lamellar separation and mandibular inter-lamellar distance (MAN model). Only two models (LS and MAN) were created for Shovelers because their maxillary and mandibular inter-lamellar distances are the same.

3.3.1.4 Implicit Model Assumptions

The models make three implicit assumptions: particles retained during one filtration cycle cannot be expelled during subsequent cycles; the presence of captured particles does not affect the probability of other particles being captured; and no water is expelled from the bill until after the maxilla and mandible are in the end position. The first two assumptions are reasonable. The lingual scrapers move particles from the lamellae to a position caudal of the lingual cushion during each cycle (Kooloos et al. 1989; Zweers et al. 1977), which will reduce clogging except at

very high particle concentrations. Because rotation of the maxilla and mandible cause water to be expelled, the third assumption is violated. As a consequence, the models will tend to over-estimate retention probabilities. This bias will be greatest when filtering small particles using large movements of the maxilla and mandible. The bias will also be greater for the Mallard model than the Shoveler model because differences in lamellar length will cause Mallard lamellar separation to remain larger over a greater range of bill movements.

3.3.2 Estimating Model Parameters and Their Relationships

To estimate the relationship between cycle volume, gape and lamellar separation, I created virtual, three-dimensional scale replicas of real duck skulls using Solidworks™, a computer-aided design application. Solidworks™ allowed me to replicate individual bones of the foraging apparatus, assemble the replica bones using joints that could be articulated realistically, and measure gape, lamellar separation and cycle volume directly from the replicas.

I created virtual replicas of skulls of a male Mallard and Northern Shoveler. Foraging performance data were available for these species and they exhibit the most divergent lamellar length and interlamellar distance of Holarctic *Anas*. Both ducks were collected in the fall near Riske Creek, British Columbia and frozen for storage. To avoid the effects of desiccation, I made a plaster cast of the interior cavity of the maxilla and mandible immediately after thawing. Replicas were created based on measurements of the original material and plaster casts made to the nearest 0.05 mm using callipers. I created two virtual models of each species, one for measuring lamellar separation and one for measuring the volume of the posterior cavity (Fig. 3.3).

I quantified the trade-off between cycle volume and particle size selection by measuring g_s , m_e , B_s , B_e , n_e and n_s from the virtual models while systematically adjusting the position of the maxilla and mandible. Contact between the maxilla and mandible and the value of d determined the range of feasible positions. I sampled this range by rotating the maxilla and mandible by a maximum of 1 and 0.5 degree increments, respectively. Parameters were always measured at mandible positions that gave maximum values of B_s at each maxilla position. Lamellar separation was measured from the most lateral edge of the dorsal mandibular lamellae to the nearest surface of the maxilla. Gape was measured as the smallest distance between the maxilla and mandible. Both lamellar separation and gape were measured to the nearest 0.01 mm from a series of points along the mandible that were a maximum of 2 mm apart.

I estimated h by measuring the thickness of the rostral edge of the lingual bulges of each duck. I estimated the values of T_s and T_e by measuring how tongue volume changes with tongue length. I measured the mass, length and volume of the tongue between the rostral ends of the lingual bulges and cushion to give its mean density. I then cut the tongue into sections, placing the cuts to maximize the homogeneity of the shape of the sections, and measured the length and mass of each section. From these data, I estimated the relationship between cumulative tongue length and volume.

3.3.3 Testing the Models

Three studies from the literature provide estimates of various performance parameters of Mallards and Shovelers foraging under controlled conditions.

Kooloos et al. (1989) measured the performance of Mallards and Shovelers foraging for 5 s on 1 g of four prey types that differed in diameter: shrimp pulp (0-0.5 mm), poppy seeds (0.7-1.2 mm), millet (1.2 – 2.4 mm) and red milo (2.6-4.4 mm). They collected the water and prey expelled by foraging ducks and estimated cycle volume and prey retention probabilities. Kooloos et al. also shortened the Shoveler's maxillary and dorsal mandibular lamellae by 3mm and the Mallard's by 1.5 and 0.5 mm, respectively, to determine the effect of lamellar length on cycle volume and retention. I duplicated their surgical manipulation by shortening the lamellae of the virtual replicas and re-estimated $R_{s,e,i}$.

Mott (1994) estimated the relationship between prey intake rate and prey density (i.e. the functional response) of Mallards and Shovelers foraging on daphnia in three size classes: small (0.4 – 0.6 mm), medium (0.8-1.0 mm), and large (1.2-1.4 mm). Mott allowed ducks to forage for 7 s from 1.47 L of water containing 50, 100, 150, 200, or 250 daphnia. Using the same techniques as Mott (1994), Tolkamp (1993) estimated the functional response of ducks foraging on large daphnia, but mixed the daphnia with detritus particles ranging in size from 0.25 to 1 mm.

For each of the foraging conditions presented in the three studies, I compared the duck's performance reported by the studies to the maximum performance predicted by the models. When ducks foraged in the presence of detritus, I estimated performance given three strategies: avoid ingesting detritus, maximize the ingestion rate of food particles and maximize energy concentration intake rate (i.e. energy $\text{ml}^{-1} \text{s}^{-1}$). Shovelers used the first strategy, while the strategy used by Mallards is unknown (Tolkamp 1993). I assumed that all particles were spherical, that the net metabolizable energy content of prey was proportional to their volume and that detritus contained no metabolizable energy. I used a particle size class width of 0.05 mm and assumed

particles were distributed equally among each size class over the particle's size range. Model results were insensitive to the value of $G_{s,i}$ since none of the studies constrained gape by using detritus that was larger than the prey. I calculated the slopes of the functional responses using an iterative version of equation 2 to account for depletion of particles, though this effect was small.

3.4 Results

Values of g_s , m_e , B_s , B_e , n_e and n_s were estimated for 53 different bill positions for the Mallard and 77 positions for the Shoveler. The filtration cycle can be started and ended at any combination of these points given $V_s > V_e$, providing a total of 1928 and 5465 performance estimates for the Mallard and Shoveler, respectively. The replicas were very accurate; the volume of the replica and plaster casts differed by less than 4%. The boundary conditions on bill positions lead to a narrow range of movement of the maxilla and mandible: 10 and 5.68 degrees, respectively, by the Shoveler and 9 and 4.81 degrees, respectively, by the Mallard. The volume of the Mallard tongue increased approximately linearly with length, while the volume per unit length of the Shoveler tongue decreased caudally (Fig. 3.4), due to the spatulate shape of the Shoveler bill and tongue (Fig. 3.3).

Shovelers and Mallards occupied similar and unique regions of performance space (Fig. 3.5). Shovelers can achieve large gapes, but are restricted to relatively low lamellar separation. Mallards are limited to smaller gapes, but can achieve greater lamellar separation. Mallard performance space falls closer to the line at which gape and lamellar separation are equal, indicating they can be more selective than Shovelers. Filtration rate of both species declined with increasing gape and lamellar separation. However, wherever the two species can achieve the same gape and lamellar separation, Shovelers can attain greater filtration rates than Mallards. Maximum filtration rates occurred at gapes of 2.5 mm for the Shoveler and at 1.9 mm for the Mallard. The slope of this 'ridge' predicts that the decline in filtration rate with increasing lamellar separation is much greater for Shovelers than Mallards. Increasing lamellar separation from each species' minimum to 1.1 mm should reduce Shoveler filtration rate 43% (58.5 ml s⁻¹ to 33.3 ml s⁻¹) compared to 25% (42.7 ml s⁻¹ to 32.2 ml s⁻¹) for Mallards. The model predicts Shovelers will be unable to elevate their tongue far enough to contact the ventral surface of the maxilla (i.e. $d > l+h$) when lamellar separation exceeds about 1.1 mm, preventing them from filter-feeding. Filter-feeding by Mallards is expected to be similarly prevented at lamellar separations greater than 2.1 mm.

The qualitative and quantitative change in particle retention with changes in prey size and lamellar length predicted by the models were in good agreement with those measured by Kooloos et al. (1989) (Fig. 3.6a, c). Only seven of 24 model estimates were outside the observed confidence intervals. Not surprisingly, the predictive ability of the models increased with prey size. The LS and MAN models tended to make the same predictions and differed from the MAX model only when ducks were feeding on shrimp or poppy seeds. The Shoveler model predicted a reduction in retention with shortening of the mandibular lamellae and no change with manipulation of the maxillary lamellae. The Mallard model predicted retention is insensitive to changes in length of either mandibular or maxillary lamellae.

Although the models correctly predicted little variation in water filtration rate (F) with variation in prey size or lamellar length, the predicted rates for both species were three to ten times greater than the rates measured by Kooloos et al. (1989) (Fig. 3.6b,d).

The slope of the functional response predicted by both species' LS and MAN models rarely differed and were in good agreement with those measured by Mott (1994) and Tolkamp (1993). Although the absolute values of the predicted slopes always under-estimated the observed values (Fig 3.7a,b), the bias was consistent among all species and treatment combinations. The MAX Mallard model predicted no retention of small or medium daphnia.

Only the strategy of not ingesting detritus predicted a change in the slope of the functional response. The decline in ingestion rate was due to reduction of both cycle volume and retention. The LS Mallard model predicted a decline in cycle volume from 2.26 ml to 1.77 ml and a decline in retention probability from 1 to 0.85. The LS Shoveler model predicted a decline in cycle volume from 4.57 ml to 2.68 ml and a decline in retention probability from 1 to 0.63. The other strategies predicted no change in cycle volume or retention and predicted ingestion of 49 to 92% of the detritus. The MAX Mallard model predicted no change in cycle volume or prey retention and no retention of detritus. The LS and MAN models accurately predicted the relative change in the slopes of the functional response for both species. For the Mallard, the model predicted a 31% decline in the slope while Tolkamp measured a 27% decline. For the Shoveler, the model predicted a 60% decline while Tolkamp measured a 51% decline.

3.5 Discussion

As predicted, and supported by the foraging experiments, bill morphology and biomechanics creates a trade-off between particle size selection and filtration rate. Increasing lamellar separation to avoid detritus results in a decline in cycle volume and water filtration rate.

This trade-off is greater for Shovelers than Mallards, primarily because of differences in length of the mandibular lamellae. Short lamellae allow Mallards to be size-selective foragers because they can achieve bill positions in which gape is similar to lamellar separation, but cycle volume is reduced and retention of small particles is decreased, particularly when cycle volume is large. Longer lamellae allow Shovelers to retain small particles even when cycle volume is large, but large differences in gape and lamellar separation limit their ability to be selective while maintaining large cycle volumes. The models predict that the trade-off between filtration rate and particle size selection should result in interspecific resource partitioning, but only given certain differences in the size-frequency distribution of prey and detritus between environments. Species should have similar preferences in some environments, particularly those with low detritus concentrations and large differences in the mean size of prey and detritus.

3.5.1 Particle Retention

The results rejected the role of the maxillary lamellae in determining particle retention by Mallards. Not only did the MAX model fail to predict retention of small and medium daphnia, it predicted detritus would pass between the lamellae and not cause a change in ingestion rate. Predicted retention probabilities of the MAX model differed from those of the LS and MAN models only when Mallards were foraging on poppy seeds. The differences between the predictions and observations were similar in magnitude, but in opposite directions. Because all the models are expected to over-estimate retention for small particles, the predictions of the LS and MAN models are more likely. Long lamellae should help to keep small particles in the bill even when the maxilla and mandible are closing. Accordingly, retention of shrimp predicted by the unmanipulated Shoveler LS model is closer to the observed value. Surprisingly, observations show Shovelers had higher retention of shrimp pulp compared to the larger poppy seeds, rather than the opposite, as predicted by the model.

Close inspection of the Mallard model and bill suggests the effective inter-lamellar distance is not fixed, but increases with lamellar separation and the size of the particles being filtered. When filtering small particles, the smallest lamellar separation is between the mandibular lamellae and the ventral surface of the maxilla (Fig. 3.8a). At greater rotations of the maxilla and mandible, the smallest lamellar separation is between the mandibular lamellae and the maxillary lamellae (Fig. 3.8b). Because maxillary inter-lamellar distance is greater than mandibular inter-lamellar distance, the effective inter-lamellar distance increases with lamellar separation. This relationship is accentuated by the triangular shape of the inter-lamellar spaces of

the maxilla, which are narrow dorsally and become wider ventrally (see Fig. 5 in Kooloos et al. 1989) and explains how Mallards are able to ingest particles smaller than their maxillary interlamellar distance (Mateo et al. 2000; Mott 1994).

3.5.2 Lamellar Manipulation

When Kooloos et al. (1989) observed that shortening of the maxillary and mandibular lamellae had no effect on retention by Mallards, they rejected sieving in favour of inertial deposition as the mechanism of retention. However, the models indicate they mistakenly expected their manipulation would affect retention. A treatment response is expected, but not for the particle sizes tested. Because the length of Mallard mandibular lamellae (0.6 mm) is smaller than the diameter of even the smallest poppy seed (0.7 mm), their treatment didn't increase lamellar separation enough to reduce retention of poppy seeds. As argued above, the maxillary lamellae do not play a role in retention of particles in the size range considered here. Kooloos et al.'s own data (their Fig. 8a) are consistent with this argument and reject the inertial deposition mechanism because poppy seeds are retained medial to the mandibular lamellae, not in the interlamellar spaces of the maxilla.

3.5.3 Cycle Volume

There were large differences between expected and predicted cycle volumes. The models over-estimated the rate at which water is expelled, but under-estimated the slope of the functional response, even for large particles that had high retention probabilities. Although differences between the predictions and data may be due to flaws in the model, this explanation cannot account for over- and under-estimates easily. Three observations suggest the foraging conditions experienced by the ducks differed between studies and from the model assumptions. First, and most importantly, the observed data do not agree. Cycle volumes measured by Kooloos et al. (1989) predict a functional response with a slope of 0.06 for both Mallards and Shovelers feeding on large daphnia without detritus, which is five (Mallard) and eight (Shoveler) times smaller than the values measured by Tolkamp (1993). Second, the absolute difference between the predicted and observed values of the slopes was very consistent between all treatment and species combinations. Third, the differences in the relative changes in slopes due to addition of detritus were in very good quantitative agreement with the data. This last comparison removes the contribution of C_i to the observed and predicted ingestion rates and indicates the ducks may have exploited greater prey concentrations than reported by Mott (1994) and Tolkamp (1993). Mott

(1994) and Tolkamp (1993) used opaque water and two air stones to keep the daphnia well mixed. The current created by the bubbler may have trapped daphnia and created local concentrations that exceeded the mean concentration in the bowl. A simple doubling of the duck's encounter rate would be sufficient to account for most of the difference in the absolute value of slopes between the observations and predictions. Alternatively, the models may be biased towards lower filtration rates than those observed by Mott and Tolkamp.

If the filtration rates observed by Mott and Tolkamp are reasonable, why did the ducks observed by Kooloos et al. (1989) expel so little water? Kooloos et al. (1989) also developed a model using the same conceptual approach as I did, but tested it differently. They observed the bill positions of the foraging ducks and used their model to predict cycle volume for those positions. Their model agreed with their observations for Mallards filtering poppy and millet seeds, but also over-estimated cycle volumes for Mallards foraging on larger seeds and Shovelers foraging on any seed size. I suspect the poor performance of both models is due to the conditions in which the ducks fed. To capture expelled water and seeds, Kooloos et al. (1989) trained their ducks to feed from a small pan that allowed only their bill tips to be submerged. Typically, ducks feed with at least half of their bill submerged (see Fig. 19 in Zweers et al. 1977). Although the tongue can act as a suction-pressure pump to move water and particles through the oral cavity (Zweers et al. 1977), filtration rates may be improved if the bill is submerged and less constrained by suction. Foraging on large seeds caused the ducks in Kooloos et al.'s (1989) study to use greater gapes, which would have further reduced the performance of the suction action of the lingual pump.

3.5.4 Foraging Strategies

Avoiding detritus was the only foraging strategy that correctly predicted a decline in Shoveler and Mallard filtration rates when detritus was present. Tolkamp (1993) found that Shovelers and Blue-winged Teal (*A. discors*) avoided ingesting detritus, but did not test if Mallards did as well. The ducks appear to be accepting reduced filtration rates to gain a reduction in the bulk of the ingesta. This strategy would be adaptive if gut capacity was a greater constraint on daily energy intake rate than the time available to forage. Ducks may not use this strategy exclusively. If the size-frequency distribution of prey and detritus overlap, which is likely in the field, ducks may be unable to avoid ingesting some detritus. In this case, ducks may optimise a more complex foraging currency involving energy concentration of the ingesta. Although both energy concentration intake rate and avoiding detritus increase when detritus is avoided, the

models predicted different behavioural responses because prey were larger than detritus. Increasing lamellar separation reduces retention probabilities of both prey and detritus, but when the currency involves a rate, the benefit of avoiding small detritus particles is less than the cost of reduced retention of larger prey particles.

3.5.5 Implications for Resource Partitioning and Community Organization

Prey size alone provides few opportunities for resource partitioning. In the absence of detritus, the ingestion rates of Shovelers will never be lower than those of Mallards. Both species should prefer habitats with abundant, large prey and respond similarly to most changes in the size-frequency distribution of prey. The only exception should occur if prey less than 0.5 mm are much more abundant in one habitat (preferred by Shovelers) than large prey are in another habitat (preferred by Mallards).

Opportunities for resource partitioning are greater when detritus is present, but both species should still prefer habitats in which prey and detritus differ in size. Species may show distinct preferences when detritus is larger than prey. Variation in gape should allow Shovelers to avoid detritus larger than 2.5 mm, while Mallards should be able to avoid detritus larger than 1.9 mm, with no effect on filtration rate. Resource partitioning should also occur when prey are small and detritus partially overlaps the lower end of the prey size distribution. Shovelers can avoid detritus as large as 1.1 mm while still maintaining higher ingestion rates than Mallards. Once detritus particles exceed a size range of 0 to 1.1 mm, Shovelers must cease foraging or begin to ingest detritus. Mallards can continue to forage while avoiding detritus until it exceeds a size range of 0 to 2.1 mm, at which point they must also cease foraging or begin to ingest detritus. Although Shovelers will always be able to maintain higher filtration rates than Mallards, the energy concentration of the particles Shovelers ingest will decline with increasing concentration of detritus 1.1 to 2.1 mm in size, while Mallards will be unaffected.

A few studies (Nudds and Bowlby 1984; Nummi 1993; Nummi et al. 1995; Nummi and Väänänen 2001) have compared invertebrate sizes in the environment to those ingested by ducks, but these data are inappropriate for testing the role of bill morphology in resource partitioning for three reasons. First, the size-frequency distribution of detritus was not measured in any study. Second, each study considered a wide range of prey sizes, even prey larger than 12.5 mm. Third, they grouped prey smaller than 2.5 mm and 2.5-7.5 mm together. Once prey become larger than 6.5 mm, Mallards switch from filter-feeding to pecking (Kooloos and Zweers 1991). Consequently, there are only two prey size classes that are relevant to filter-feeding.

The conflicting results of field studies that have attempted to test for indirect evidence of prey size partitioning by comparing species distributions between and within ponds (Elmberg et al. 1993; Elmberg et al. 1994; Nudds et al. 2000; Nudds et al. 1994; Nudds and Wickett 1994; Osnas and Ankney 2003; Pöysä et al. 1994; Pöysä et al. 1996) may be due to false assumptions. All of these studies assumed bill morphology leads to distinct habitat preferences among species, and, therefore, constant associations between species and habitats. If species share some habitat preferences, as predicted by the models, then species may utilize the same habitat under some conditions and different habitats under other conditions (Guillemain et al. 2002; Rosenzweig and Abramsky 1986).

The trophic apparatus of dabbling ducks is a dynamic system with some flexibility to reduce apparent morphological limitations and adapt to different foraging environments. Interspecific variation in bill morphology allows partitioning of foraging resources among two species of dabbling ducks, but the performance trade-offs predict shared habitat preferences among species, rather than distinct preferences, as many earlier studies assumed. Shared preferences will make testing the implications of bill morphology for community structure more difficult. Future field studies will have to predict the expected distribution of species among habitats directly from the size-frequency distribution of prey and detritus given each species' morphology.

Table 3-1 Parameters used in the models, their symbols, description, and units. Values for Mallards and Shovelers are given if the parameters were assumed to be constant or had maximum values.

Symbol	Parameter Description	Value	
		Mallard	Shoveler
B_e	Volume of the posterior cavity at end position e (ml)		
B_s	Volume of the posterior cavity at start position s (ml)		
C_i	Concentration of particles in size class i in the environment (ml^{-1})		
d	Maximum separation between maxilla and mandible at which filtration occurs (mm)	9.63	11.25
e	Position of the maxilla and mandible at the end of a cycle		
F	Water filtration rate (ml s^{-1})		
$G_{s,i}$	Probability of a particle in size class i passing through the gape at start position s		
g_s	Gape at start position s (mm)		
h	Thickness of the lingual bulges when depressed (mm)	3.63	5.25
I	Particle ingestion rate (particles s^{-1})		
i	Particle size class		
j	Distance from the tip of the mandible to the caudal end of the region of water expulsion (mm)	41	49
k	Distance from the tip of the mandible to the rostral end of the region of water expulsion (mm)	56	66.5
l	Maximum elevation of the lingual bulges (mm)	6	6
$M_{e,i}$	Probability of a particle in size class i passing through the lamellae at end position e		
m_e	Lamellar separation at end position e (mm)		
n_e	Distance from the tip of the mandible to the rostral end of the lingual bulges at end position e (mm)	15	18
n_s	Distance from the tip of the mandible to the rostral end of the lingual bulges at start position s (mm)	27.5	36
$R_{s,e,i}$	Retention probability for particles in size class i given a cycle from start position s to end position e		
s	Position of the maxilla and mandible at the start of a cycle		
T_e	Volume of tongue in the posterior cavity at end position e (ml)		
T_s	Volume of tongue in the posterior cavity at start position s (ml)		
V	Cycle volume (ml)		
V_s	Volume of the posterior cavity at start position s (ml)		
V_e	Volume of the posterior cavity at end position e (ml)		
x	Distance along mandible from tip (mm)		
Z	Cycle rate (s^{-1})	18	13
z	Number of particle size classes		
	Maxillary interlamellar distance (mm)	1.0	0.3
	Mandibular interlamellar distance (mm)	0.6	0.3

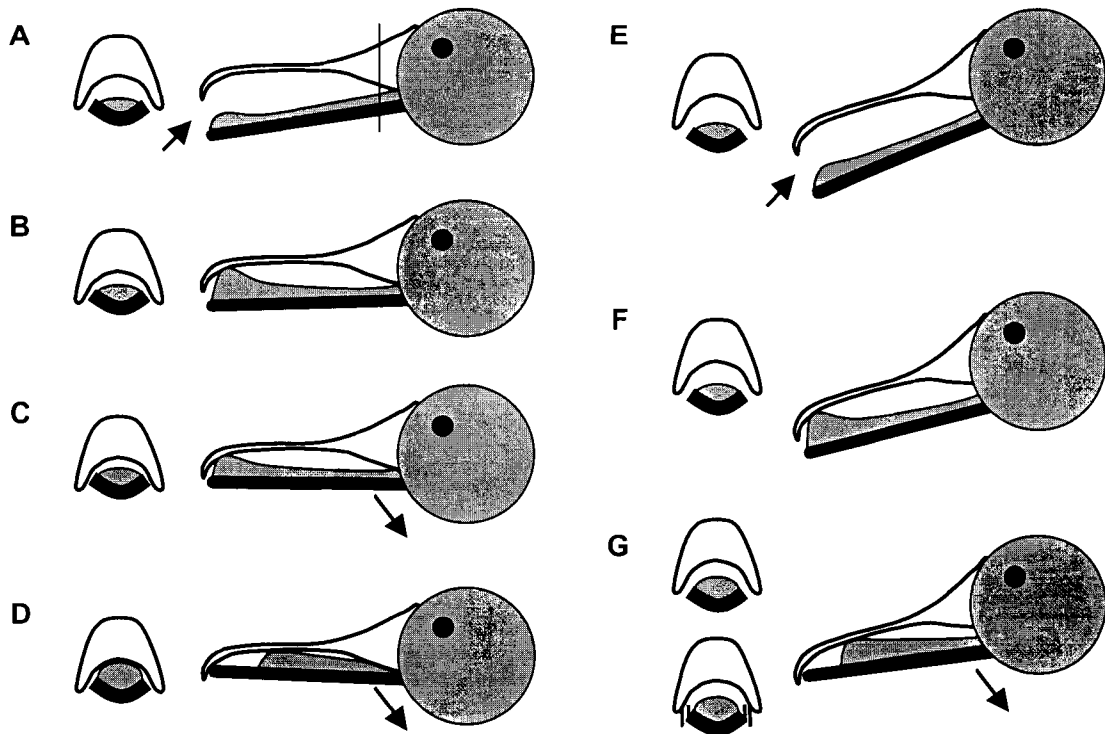


Figure 3-1 The biomechanics of filter-feeding by dabbling ducks. Illustrations show cross-sections (left) and sagittal sections (right) of the maxilla (clear), mandible (solid) and tongue (gray) at different points during the filtration cycle. The cross-section is located at the caudal end of the bill where particles are filtered (vertical line in A). (A) At the start of the filtration cycle the mandible is depressed and water and prey are drawn into the bill through the gape (arrow). (B) The mandible and the lingual bulges are elevated. The bulges contact the ventral surface of the maxilla, which traps water and prey in the bill. (C) The mandible continues to elevate, which decreases the volume of the cavity posterior of the lingual bulges, forcing water out the posterior, lateral margins of the bill (arrow). (D) At the end of the cycle, the mandible is fully elevated, the tongue is fully retracted and the volume of the posterior cavity is minimized. The mandible is then depressed, the tongue protracts and the cycle is repeated. Cycle volume is maximized when gape is at a maximum at the start of the cycle and lamellar separation is minimized at the end of the cycle. To ingest a smaller size range of particles, either gape must be reduced (start at B), or lamellar separation must be increased (end at C), which will reduce cycle volume. Lamellar separation can also be increased by filter-feeding with the maxilla in a depressed condition (E-G), but cycle volume is also reduced. Lamellar separation (see Fig. 3.2) is less sensitive to changes in mandible position in species with long lamellae (compare cross sections in G).

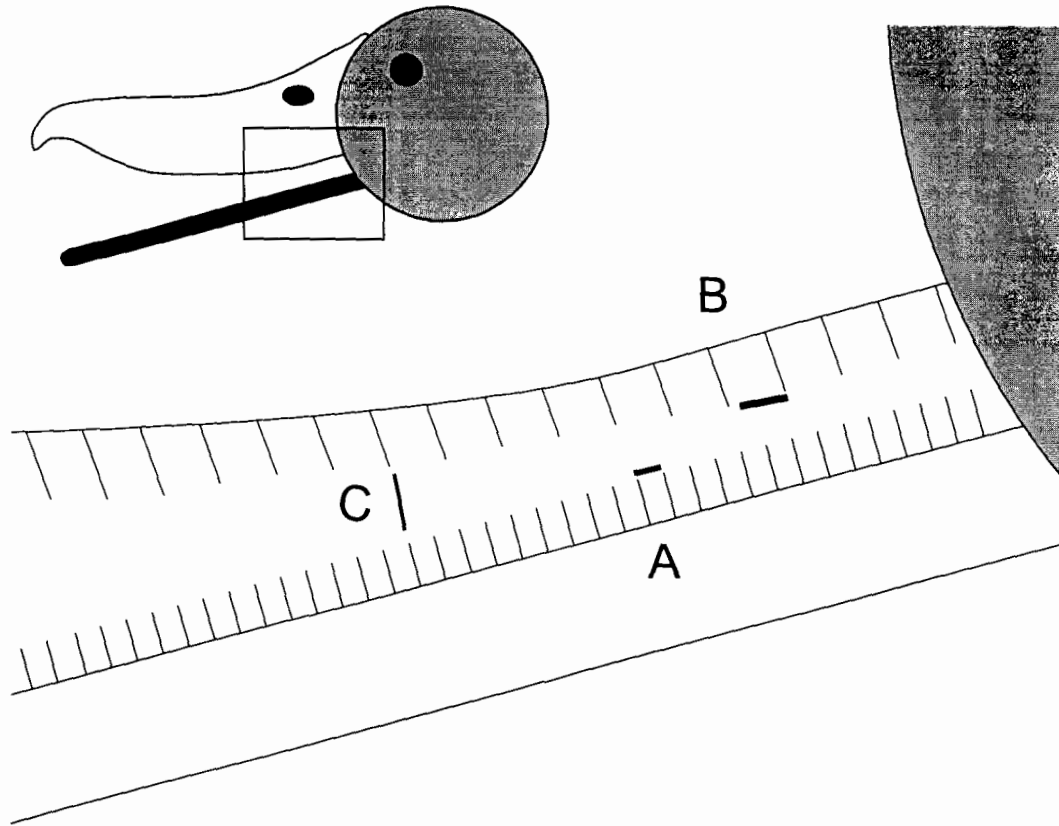
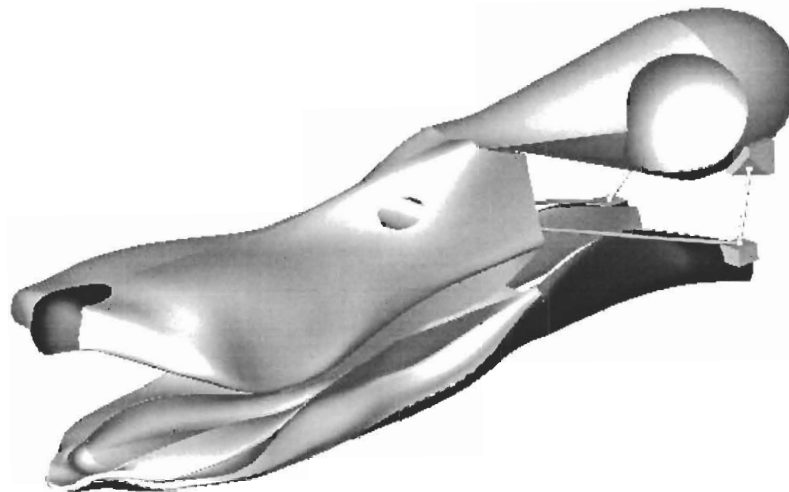


Figure 3-2 Detail of the lamellar filter of dabbling ducks. Inter-lamellar distance is the distance between adjacent lamellae on the mandible (line segment A) or the maxilla (line segment B). Lamellar separation is defined as the distance between lamellae on the maxilla and mandible (line segment C). Lamellar separation can vary with distance along the length of the bill and may be greater or less than maxillary or mandibular inter-lamellar distance depending on the position of the maxilla and mandible.

A



B

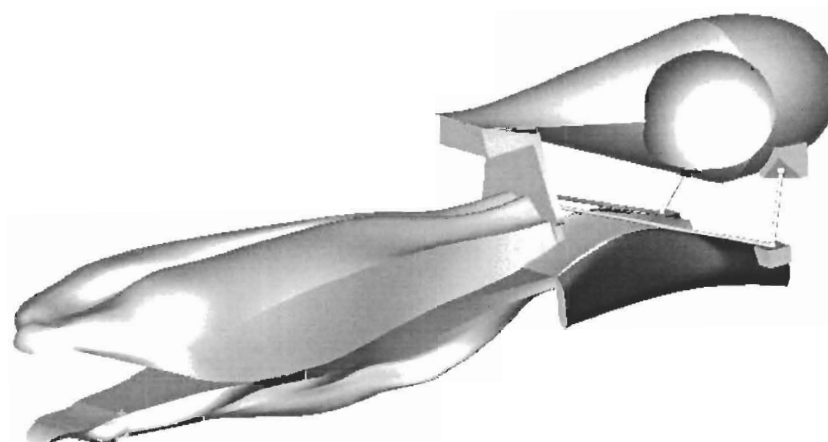


Figure 3-3 Three dimensional, scale replicas of a Shoveler skull generated using Solidworks™. (A) The skull with the replica maxilla and mandible for measuring gape and lamellar separation. (B) The skull with the replica casts of the interior cavities of the maxilla and mandible for measuring volume of the posterior cavity.

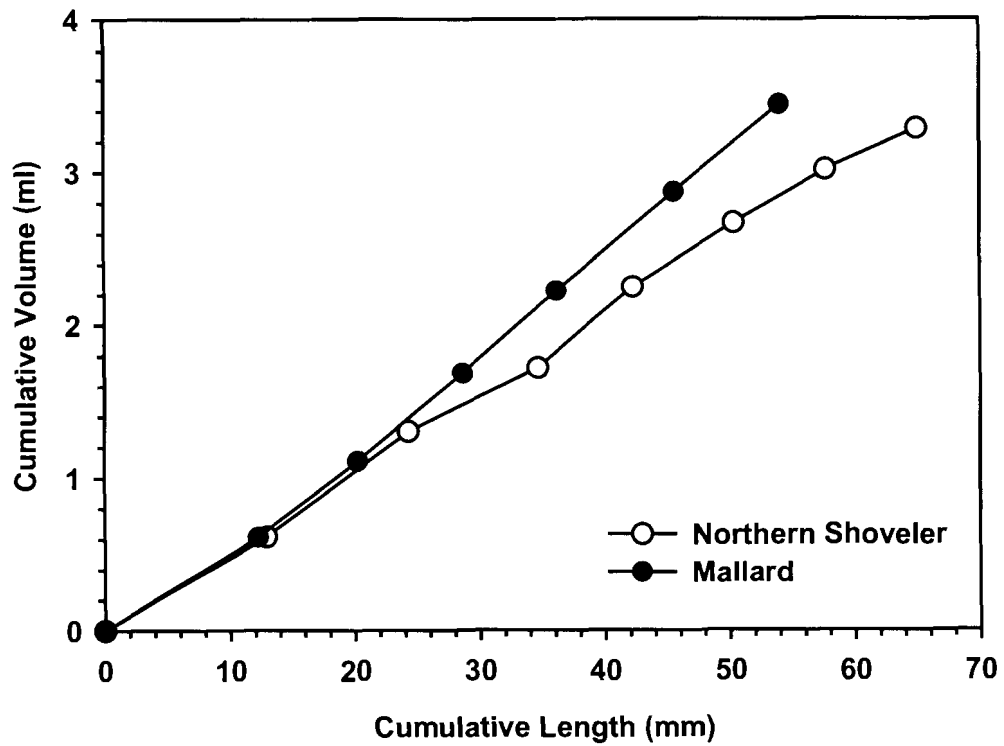


Figure 3-4 The increase in cumulative tongue volume with cumulative tongue length for two species of dabbling ducks. Maximum length was measured between the rostral end of the lingual bulges and the rostral end of the lingual cushion. Linear interpolation was used to estimate values between data points.

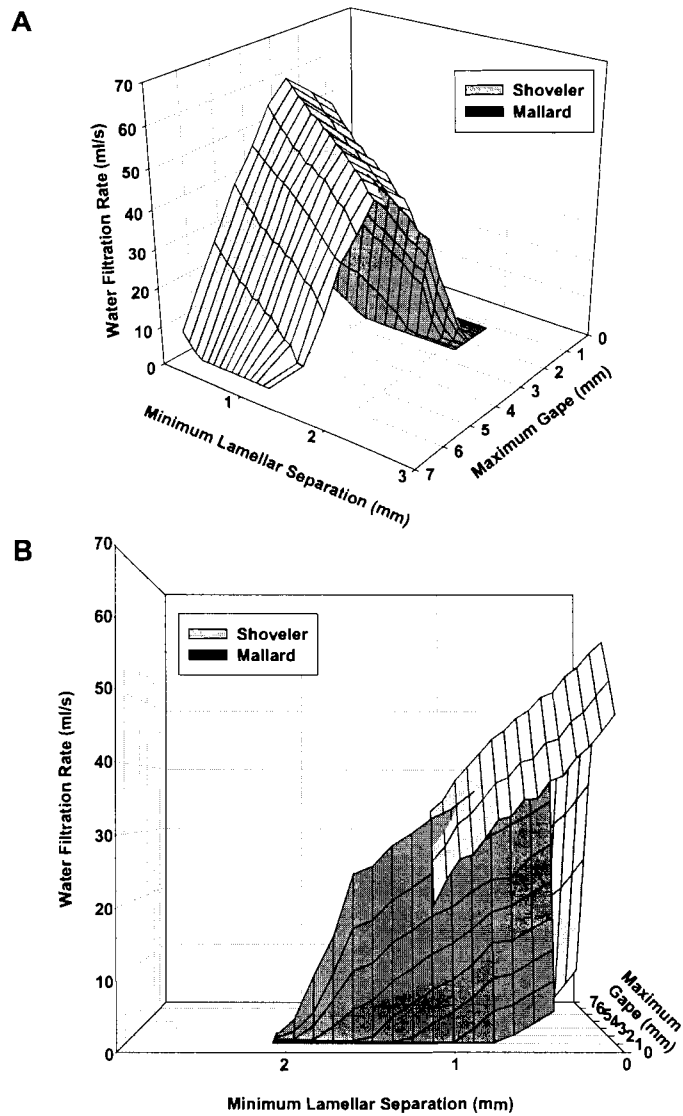


Figure 3-5 Constraints of morphology and biomechanics on filter-feeding performance by two species of dabbling ducks in an isometric view (A) and emphasising the effect of increasing lamellar separation (B). Each species' total performance space forms a volume, but only values that give maximum filtration rates are plotted, revealing a performance surface. Maximum gape and minimum lamellar separation are plotted to show the consequences of avoiding detritus particles on filtration rate.

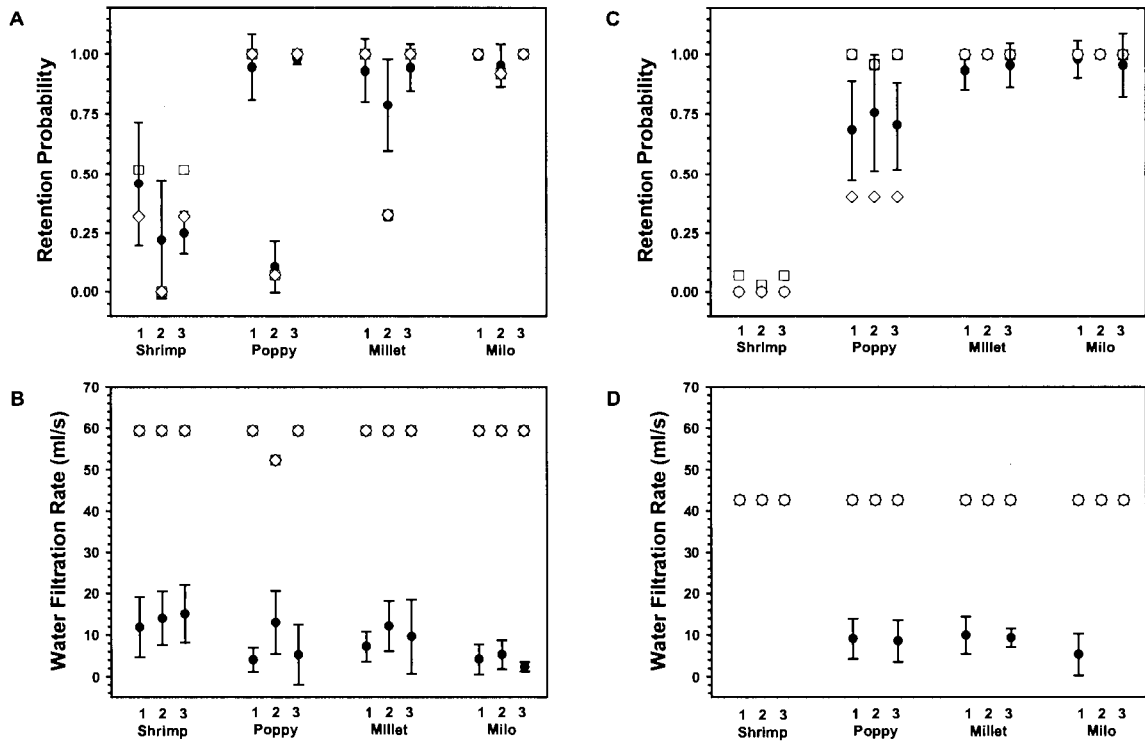


Figure 3-6 Comparison of predicted (open symbols) and observed (dark circles) performance parameters for Shovelers (A, B) and Mallards (C, D) filter-feeding on pulverized shrimp, poppy seed, millet seed and milo seed (particle size increases from left to right). Error bars indicate 95% confidence intervals. Open symbols give model predictions depending on which trait constrains the lower limit of particle retention: lamellar separation (square), maxillary interlamellar distance (diamond), and mandibular interlamellar distance (circle). The maxillary and mandibular interlamellar distance of Shovelers are equal, so these model predictions are indicated by a single symbol (diamond). 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. No observations are reported for the following treatment combinations for Mallards: water expulsion for poppy 2; water expulsion and retention for millet 2 and for milo 2 and 3. Observed data are from Kooloos et al. (1989).

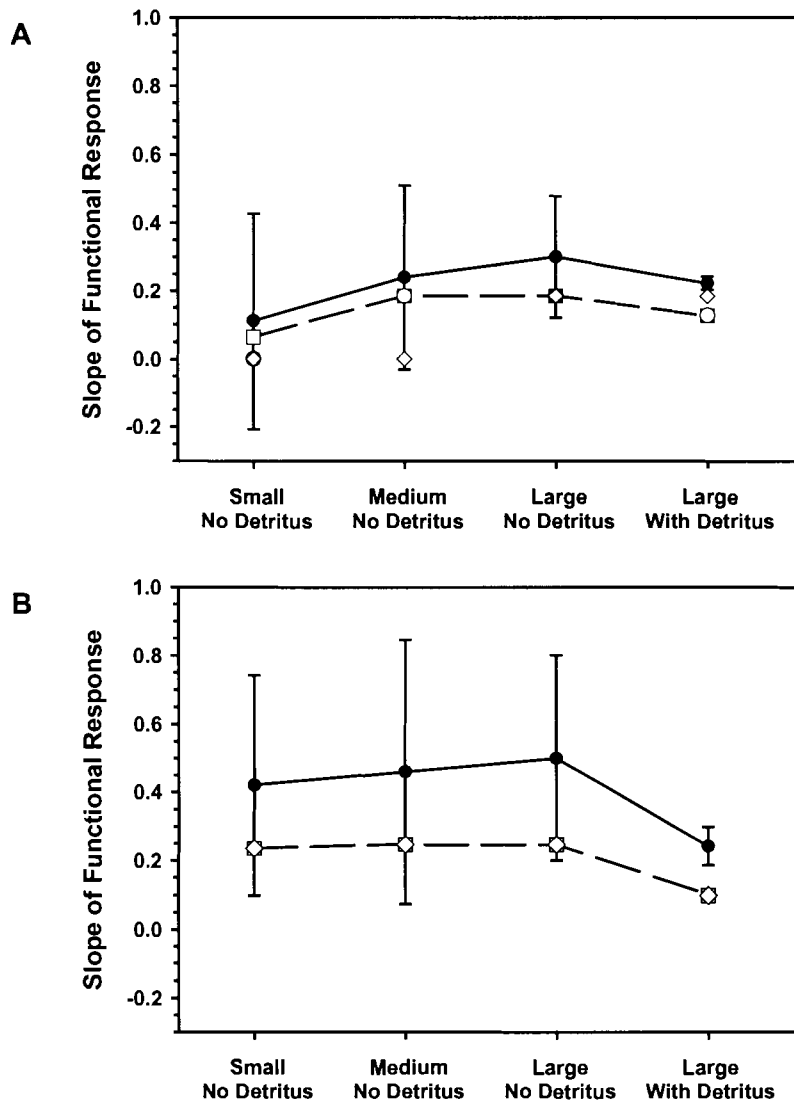


Figure 3-7 Comparisons of predicted (open symbols) and observed (dark circles and solid line) slopes of type I functional responses of Mallards (A) and Shovelers (B) filtering daphnia of three different sizes with or without detritus. Error bars indicate 95% confidence intervals. Open symbols give model predictions depending on which trait constrains the lower limit of particle retention: lamellar separation (square and dashed line); maxillary interlamellar distance (diamond); or mandibular interlamellar distance (circle). The maxillary and mandibular interlamellar distance of Shovelers are equal, so these model predictions are given by a single symbol (diamond). All model predictions assume ducks forage to avoid ingesting detritus. Observed data are from Mott (1994) and Tolcamp (1993).

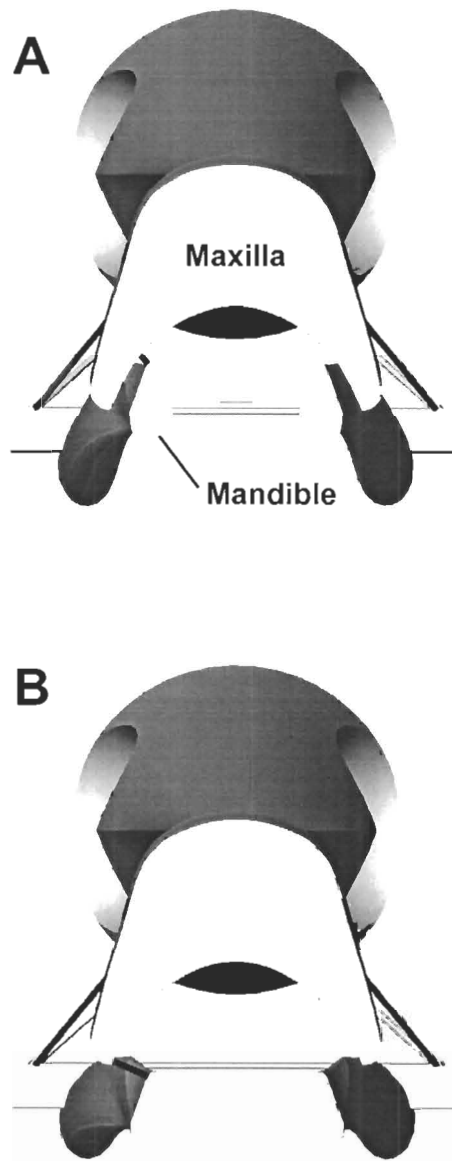


Figure 3-8 Cross-sections of the maxilla and mandible of the Mallard model showing the change in the location of particle retention with increasing lamellar separation of Mallards. (A) When lamellar separation is small, the shortest distance is between the dorsal mandibular lamellae and the ventral surface of the maxilla (dark line), where the inter-lamellar space is narrow. (B) When lamellar separation is large, the shortest distance is between the dorsal mandibular lamellae and the ventral edge of the maxillary lamellae (dark line), where the inter-lamellar space is wide.

CHAPTER 4 PREDICTING INTERSPECIFIC RESOURCE PARTITIONING AND HABITAT PREFERENCE OF FILTER-FEEDING DABBING DUCKS FROM FUNCTIONAL MORPHOLOGY

4.1 Abstract

The ecological theory of adaptive radiation proposes that divergent natural selection on phenotypic traits between populations in different environments promotes ecological diversity and results in speciation. Competition for resources can result in divergent selection if phenotypic traits interact with the environment to produce trade-offs in the ability of individuals to exploit different resources. Dabbling ducks (*Anas* spp.) may be an example of an adaptive radiation caused by divergent selection on bill morphology, but current evidence is contradictory. To test if bill morphology imposes performance trade-offs on filter-feeding ducks in different environments, I developed biomechanical models to predict the net energetic rates for seven species of ducks. The models predict that all seven species face a trade-off between prey size selection and filtration rate. Size-selective foraging is beneficial when the size-frequency distribution of prey and detritus particles differ. Bill morphology determines the form of the trade-off and the size range of prey each species can filter at the highest rate, leading to interspecific partitioning of prey by size. The models provide limited support for the predictions tested by earlier studies, suggesting the conflict between results was due to incorrect assumptions. The models also predict dabbling ducks should exhibit shared and distinct habitat preferences, consistent with the centrifugal model of community organization. Results suggest that adaptive processes drove the radiation of species within the genus *Anas*. However, stronger conclusions must await more thorough testing of the models.

4.2 Introduction

The ecological theory of adaptive radiation proposes that divergent natural selection on phenotypic traits between populations in different environments promotes ecological diversity (Schluter 2000) and results in speciation (McKinnon et al. 2004; Schluter 2001). Competition for resources can result in divergent selection if phenotypic traits interact with the environment to produce trade-offs in the ability of individuals to exploit different resources (Doebeli 1996; Taper and Case 1992). Trade-offs cause selection to increase fitness in one environment while reducing fitness in other environments. Consequently, the ecological theory predicts that closely related species will exploit resources in at least one environment more efficiently than all other species, leading to resource partitioning between species.

Dabbling ducks form a monophyletic clade (Johnson and Sorenson 1998) and may be an example of an adaptive radiation (Schluter 2000) caused by divergent selection on bill morphology (Darwin 1998; Lack 1971; Lack 1974). Interspecific variation in bill morphology is thought to influence filter-feeding performance, leading to size-based partitioning of prey (Crome 1985; Kooloos et al. 1989; Mott 1994; Nudds and Bowlby 1984; Nudds et al. 1994; Nudds and Wickett 1994). Dabbling ducks are distributed non-randomly among wetlands (Nudds and Wickett 1994; Osnas and Ankney 2003; Pöysä et al. 1994; Pöysä et al. 1998) and studies have attempted to infer resource partitioning through correlations between bill morphology and use of habitats that differ in prey size, but results have been contradictory. Some correlations have been interpreted as consistent with the bill morphology hypothesis (Nudds et al. 2000; Nudds et al. 1994), while others have not (Elmberg et al. 1993; Elmberg et al. 1994; Osnas and Ankney 2003; Pöysä et al. 1994; Pöysä et al. 1996). However, evidence for and against the bill morphology hypothesis has been criticized, primarily because expectations of which habitats should provide species with the best foraging performance have been based on a weak understanding of the performance trade-offs imposed by the interaction between morphology and environmental conditions (Chapter 1).

In Chapter 3 I used explicit models of bill biomechanics to predict the filter-feeding performance of Mallards (*A. platyrhynchos*) and Northern Shovelers (*A. clypeata*) under different environmental conditions. Two previously separate ideas were synthesized in these models. First, the models allowed the environment to contain detritus particles with low energetic value, which would reduce energetic intake rates if they were ingested. Ducks are able to avoid detritus when prey and detritus differ in size (Tolkamp 1993; Van Eerden and Munsterman 1997, Chapter

2), but experience a simultaneous decline in foraging rates (Tolkamp 1993; Van Eerden and Munsterman 1997). Second, the models allowed ducks to adjust the position of the maxilla and mandible, which affects the size of particles retained during feeding (Kooloos et al. 1989). The synthesis of these ideas correctly predicted a trade-off between filtration rate and prey size selection mediated by bill morphology (Chapter 3).

In this paper, I develop models for five additional species of sympatric dabbling ducks to test if the performance trade-off imposed by the interaction between bill morphology and environmental conditions allow resources to be partitioned among all seven species. I also test whether shared habitat preferences are a general characteristic of the larger community. Finally, I test whether the correlations between bill morphology and habitat use predicted in earlier studies are supported by the models.

4.3 Methods

4.3.1 Filter-Feeding Biomechanics

Dabbling ducks filter-feed using bill and lingual movements to create a flow of water that enters the bill at the distal end of the maxilla and mandible (gape) and exits through the space between the lamellae lining the posterior, lateral margins of the maxilla and mandible (Kooloos et al. 1989; Zweers et al. 1977). The size of the space between the lamellae is a function of lamellar spacing and the separation between lamellae on the maxilla and mandible. The position of the maxilla and mandible at the start of the filtration cycle, when water and particles enter the bill, determines the gape. The position of the maxilla and mandible at the end of the cycle, when water is forced out of the bill, determines the separation of the lamellae. Particles that are smaller than the gape, but larger than the lamellar separation and lamellar spacing, are retained and ingested (Chapter 3). Fast, repeated cycles of movement of the tongue, maxilla and mandible allow ducks to filter large volumes of water quickly.

While filter-feeding, dabbling ducks are faced with the challenge of ingesting prey particles (seeds and invertebrates) while avoiding detritus particles of low energetic value (silt, sand and dead plant material) (Bethke and Nudds unpublished; Tolkamp 1993; Van Eerden and Munsterman 1997). By varying the position of the maxilla and mandible at the start and end positions, ducks can adjust both gape and lamellar separation (Kooloos et al. 1989; Zweers et al. 1977) to select particles by size and maximize the energy density of the ingested particles (Chapters 2 and 3). However, filtration rates decline when the size range of particles ingested is

reduced because the volume of water filtered per stroke of the tongue is decreased (Chapter 3). Bill morphology constrains the combinations of gape, lamellar separation and filtration rate each species can achieve (Chapter 3). Consequently, species should choose habitats that optimize the trade-off between reduced filtration rate and net energy density of the particles ingested. To assess the influence of this trade-off on foraging performance in different environments, I constructed a model that estimates the ability of each species to meet their daily energetic needs by foraging in environments that differed in the size-frequency distribution of prey and detritus.

4.3.2 The Model

The daily net energy (E_N kcal) available to a duck is the difference between the daily energy expended (E_E) and the daily energy gained through filter-feeding (E_G)

$$E_N = E_G - E_E \quad 1$$

The energy gained through filter-feeding is given by

$$E_G = PHE_M t \quad 2$$

where P is the total prey intake rate (ml s^{-1}), H is the density of prey (g ml^{-1}), E_M is the metabolizable energy content (kcal g^{-1}) of prey and t is the time (s) spent foraging. When foraging on a mixture of prey and detritus particles of size $i=1, 2, 3, \dots, z$

$$P = \sum_{i=1}^z C_{Pi} V_i (V_s - V_e) Z R_{s,e,i} \quad 3$$

and the total detritus intake rate ($D \text{ ml s}^{-1}$) is

$$D = \sum_{i=1}^z C_{Di} V_i (V_s - V_e) Z R_{s,e,i} \quad 4$$

where V_i is the volume (ml) of a particle of size i , $V_s - V_e$ is the volume (ml) of water filtered when the maxilla and mandible start the filtration cycle at position s and end at position e , Z is the lingual cycle rate (s^{-1}), $R_{s,e,i}$ is the retention probability of particles of size i given start position s and end position e , and C_{Pi} and C_{Di} are the concentrations (particles ml^{-1}) of prey and detritus of size i , respectively, in the environment (Chapter 3). The value of E_G is limited by the maximum volume (V_{MAX}) of ingesta the gut can process in time t such that

$$(P + D)t \leq V_{MAX} \quad 5$$

4.3.3 Parameter Estimation

Parameter values for Mallards and Shovelers were taken from Chapter 3. I estimated the values of V_s , V_e , and $R_{s,e,i}$ for five additional species of dabbling ducks: a male Northern Pintail (*A. acuta*), a male American Wigeon (*A. americana*), a female Blue-winged Teal (*A. discors*), a female Green-winged Teal (*A. crecca*), and a male Gadwall (*A. strepera*) using methods described in Chapter 3. The following provides a brief description of these methods, but readers should refer to Chapter 3 for more detail. I used computer-aided design software (Solidworks™ 2001) to create digital, three-dimensional replicas of each species' skull. The maxilla and mandible of the replicas were placed in a series of start and end positions. At each position, the shape of the gape and the space separating the lamellae was quantified. The probability that a particle of size i would pass through the gape, and be retained by the lamellae, was calculated from these shapes. The spacing of the mandibular lamellae sets the minimum size of a particle that can be retained (Chapter 3). I used the mean of ten measurements of the spacing of the mandibular lamellae to estimate values of i for which $R_{s,e,i}=0$ (Table 1). The volume enclosed by the bill was also estimated at each start and end position. The difference between these volumes, minus the volume of the tongue, gives an estimate of the volume of water filtered per cycle. The maximum value of V_s and V_e are determined, in part, by the ability of the tongue to retract and elevate (parameters n_s-n_e and l , respectively, in Chapter 3) during the filtration cycle. These parameters are not known for species other than Mallards and Shovelers, so I assumed they were directly proportional to the length of the maxilla (Table 1). I assumed the lingual cycle rate was the same for all species and equal to 19 ml s^{-1} , the mean cycle rate of Mallards (Kooloos et al. 1989).

The values of V_{MAX} , E_E and E_M were estimated using relationships taken from the literature. Mallards fed a low quality commercial diet of alfalfa consumed 97.4 g day^{-1} (Miller 1975). A different commercial diet with a similar nutrient content had a density of 1.19 g ml^{-1} , giving an intake rate of 82 ml day^{-1} . The relationship between total gut mass (kg) and body mass ($M \text{ kg}$) of 18 species of geese and ducks is $1.82M^{1.07}$ ($F=51.9$ $p<0.001$ $R^2=0.76$) (data from Barnes and Thomas 1987). Because mass scales proportionately to volume, I estimated that the allometric relationship between maximum gut processing rate ($V_{MAX} \text{ ml day}^{-1}$) and body mass was $V_{MAX}=69.5M$. Bruinzeel et al. (1997) combined data from a number of studies and estimated the rate of energy expenditure for waterfowl as $170M^{0.68}$ (kcal/day). The digestibility of food is a function of the time ingesta is retained in the gut. Birds do not alter the passage rate of digesta when food quality decreases or energetic demands increase (Dykstra and Karasov 1992; Karasov

1990; McWilliams et al. 1999). Accordingly, passage rate is constant among waterfowl of different body sizes (Bruinzeel et al. 1997). Instead, birds increase retention time by increasing gut length (Drobney 1984; Dykstra and Karasov 1992; Miller 1975). Among waterfowl the allometric relationship between M and total gut length L (cm) and retention time H (s) is $176.8M^{0.24}$ and $8427M^{0.22}$, respectively (Bruinzeel et al. 1997). The maximum true metabolizable energy obtained by Mallards from seeds of 14 different native plants commonly consumed by ducks is 3.1 kcal g^{-1} (Kaminski et al. 2003). Mallard body mass is 1.18 kg (Nudds et al. 1994), therefore, I estimated the metabolizable energy content of prey as $E_M = 3.0 M^{0.24}$. I assumed $E_M = 0$ for detritus and that prey density was 1.2 g ml^{-1} , equal to the density of corn.

4.3.4 Size-frequency Distributions of Prey and Detritus

To facilitate programming of the models, I used two different methods to describe the size-frequency distribution of prey and detritus. Both methods describe similar distributions in which small particles are far more abundant than large particles. In method A the concentration of prey and detritus particles were given by

$$C_{Pi} = \Delta_P / zV_i \quad 6$$

and

$$C_{Di} = \Delta_D / zV_i \quad 7$$

where Δ_P and Δ_D give the proportion, by volume, of the foraging medium composed of prey and detritus, respectively. Equations 6 and 7 ensured each size class contained an equal total volume of particles. The size-frequency distribution was further constrained by the requirement that $\Delta_P + \Delta_D < 1$. Method B assumed the size-frequency distribution of prey and detritus followed a log-normal distribution as shown by Mittlebach (1981) for aquatic invertebrates. The distribution for prey is given by

$$C_{Pi} = j e^{-\ln\left(\frac{d_i}{k}\right)^2 / 2m^2} \quad 8$$

and for detritus by

$$C_{Di} = q e^{-\ln\left(\frac{d_i}{r}\right)^2 / 2u^2} \quad 9$$

where j and q are the maximum particle frequencies, k and r are the mean particle diameters and m and u are the standard deviation of particle sizes, for prey and detritus respectively, and d_i is the diameter of particles in size class i . Both methods divided prey and detritus particles into 88 size

classes ranging from 0.025 mm to 4.375 mm. I assumed both prey and detritus particles were spherical.

4.3.5 Simulations

To assess how foraging performance should vary with changes to environmental conditions, I conducted four series of simulations that imposed different constraints on the size-frequency distribution of prey and detritus. For each distribution, I calculated the maximum net daily intake rate (E_N) each species could achieve given the bill positions at which I measured model parameters. If different bill positions gave the same energetic rate, I report the value that also minimized the time spent foraging (t).

The first series of simulations determined how foraging performance varies with prey concentration in the absence of detritus. Prey occurred in all size classes and the size-frequency distribution was defined by method A. The second series determined how foraging performance of each species varied with prey size in the absence of detritus. Prey were constrained to occur in only one size class. The frequency of prey in each size class was defined by method A. The third series determined how foraging performance of each species varied with Δ_P , Δ_D and prey size in the presence of detritus. The frequency of prey and detritus in each size class was defined by method A. Detritus occurred in all size classes, but prey were constrained to occur in only one size class as in the second simulation. High performance in this simulation indicated the ability to separate a single size class of prey from a wide distribution of detritus particles. The fourth series tested whether the models supported the correlations between environmental conditions and habitat choice predicted by previous studies. Nudds et al. (1994) predicted that ducks with narrow lamellar spacing should forage in deep-water habitats where invertebrate prey are smaller, while species with wide spacing should forage in shallow-water habitats where invertebrates are larger. Nudds et al.'s (1994) prediction did not consider detritus, but I allowed detritus size to decline along the water-depth gradient as suggested by others (Bethke and Nudds unpublished; Tolkamp 1993). Pöysä et al. (1994) predicted that competition between species should limit assemblages to species with the most divergent morphological traits relevant to resource partitioning when prey abundance or prey size variability declines. To test these three predictions, I simulated a series of habitats that represented a gradient in the relevant parameter of the log-normal size-frequency distribution of prey and detritus and calculated each species' net energetic rate in each habitat along the gradient.

4.4 Results

4.4.1 Functional Morphology

The biomechanical models predicted a number of similarities and differences in the performance surfaces that relate bill form with function among the seven species (Fig. 4.1). All seven species had one combination of gape and lamellar separation at which they achieved their greatest filtration rate, either when gape is at a maximum or lamellar separation is at a minimum. Each species thus faces a performance trade-off because reducing gape and/or increasing lamellar separation to ingest a smaller range of particle sizes forces a decrease in filtration rate. The shape of the performance surfaces of Mallards, Shovelers, Pintails and Gadwalls are all similar and feature a ridge of maximum filtration rate running parallel to the lamellar separation axis. For these species, changes in gape have less of an effect on filtration rate than changes to lamellar separation because of their longer bills. In contrast, the ridge of maximum filtration rate for Blue-winged Teal runs parallel to the gape axis. The performance surfaces of Wigeon and Green-winged Teal fall in between these two extremes. Surfaces for both species have two ridges, one running parallel to each of the gape and lamellar separation axes. Changes in gape and lamellar separation have more similar effects on filtration rate for these species because they possess shorter bills.

In spite of these differences, the models predicted that only Shovelers, Mallards, Pintails, Gadwall and Wigeon can achieve a greater filtration rate than all other species at some combination of gape and lamellar separation (Fig. 4.1h). The filtration rate of Shovelers was always greater than that of every other species at every combination of maximum gape and minimum lamellar separation Shovelers could achieve. The two Teal species never achieved the greatest filtration rate at any combination of gape and lamellar separation. Mallards, Gadwall, Pintails and Wigeon achieved greater filtration rates only when lamellar separation was greater than 1 mm, which Shovelers could not achieve.

In general, the position of each species in parameter space, and the extent of parameter space it occupies, was related to the length of the maxilla and mandible. Species with short bills, such as the two Teal species and Wigeon, occupied a smaller region of parameter space and were located closer to the origin. Although Shovelers possess the longest bills, the models predict they can not increase lamellar separation as much as Pintails, Mallards, Gadwall or Wigeon and still filter-feed. Shovelers possess lamellae that are much longer than the other species. The lamellae overlap when the bill is in most positions, which limits lamellar separation. Only when the

separation between the maxilla and mandible is wide, and near the limiting value of d , does lamellar separation increase.

4.4.2 Simulation 1

When prey concentration increases in the absence of detritus, Shovelers and Pintails were predicted to achieve net energetic rates greater than all other species, but only over a very small range of concentrations (Fig. 4.2a). Mallards should have the highest intake rates over most concentrations (Fig. 4.2a). Shovelers were predicted to be the most efficient foragers at low prey concentrations (Fig. 4.2b) because they have low energy requirements and high filtration rates given their body mass, in spite of consuming smaller prey (Fig. 4.2d) over a narrower size range (Fig. 2c). Pintails, and eventually Mallards, were predicted to perform better at higher prey concentrations because they have larger gut volumes and can extract more energy from their prey, but are limited by foraging time at low prey concentrations. The greatest overlap in prey sizes consumed was predicted to be between Mallards, Gadwall, Pintail and Blue-winged Teal, all of which should prefer prey 0.8 to 1.2 mm in diameter (Fig. 2d).

4.4.3 Simulation 2

Limits to gape and lamellar separation and lamellar spacing limit the size of prey each species is capable of filtering. Shovelers can achieve the largest gapes and the lowest lamellar separation (Fig. 4.1). Consequently, in the absence of detritus, they should be able to filter not only the widest range of prey sizes, but also the largest and smallest prey (Fig. 4.3a). Pintails can filter the next widest range of prey sizes, followed by Mallards, while Blue-winged Teal should be limited to the smallest size range (Fig. 4.3a). Interestingly, the models predicted the two Teal species could not achieve positive net energetic rates, even when prey size or concentration were high enough that foraging time did not limit intake rate (Fig. 4.3a,b). In each simulation prey were limited to one size class, but all seven species minimized their foraging time when filtering prey 0.6-1.3 mm in diameter (Fig. 4.3b).

4.4.4 Simulation 3

Combining prey and detritus together had a number of effects on the predictions of the models. As expected, detritus reduced the net intake of each species by diluting the energy content of the ingesta. Detritus also reduced the size range of prey each species could profitably consume. In the absence of detritus, Shovelers achieved a positive net intake rate from ingesting

prey ranging in size from 0.125 mm to over 4.375 mm, with prey of 0.925 mm being the most profitable (Fig. 4.3a). In the presence of detritus, Shovelers could profit only from prey 0.325 mm to 1.225 mm in size (Fig. 4.4d), with prey of 0.475 mm being the most profitable. In the absence of detritus the most profitable prey size for Mallards and Pintails was 1.025 mm and 1.475 mm, respectively (Fig. 4.3a). In the presence of detritus the most profitable prey increased in size to 1.925 mm and 2.375 mm, respectively (Fig. 4.4d). Variation in Δ_p and Δ_D affected the energetic rate achieved from each size class, but did not alter which prey size was the most profitable (Fig. 4.4). The net effect of detritus was to reduce the amount of overlap between species in the size of prey they could profitably exploit. The reduction in overlap was greatest among the species with long bills: Shoveler, Gadwall, Mallard and Pintail. Wigeon exhibited a lot of overlap with Shovelers and Gadwall and the two Teal species overlapped each other extensively. However, the peak in the energetic rates of the two Teal species corresponded with low energetic rates for Wigeon, Gadwall and Mallards.

4.4.5 Simulation 4

Variation in the mean size of prey and detritus had little effect on the energetic rates of Mallards, Pintails, Shovelers or Gadwalls, regardless of whether prey size was equal to, larger than, or smaller than, detritus size (Fig. 4.5a,b,c). Although energetic rates of Wigeon and the two Teal species increased with decreasing prey size, the energetic rate of all seven species was maximized in the same habitat. Energetic rates of all seven species were more sensitive to differences in the mean size of prey and detritus, but there was little evidence this variation lead to resource partitioning. All species preferred the same habitat when prey size varied more between habitats than detritus size (Fig. 4.5d). When detritus size varied more between habitats than prey size the models predicted only Wigeon would maximize its energetic rate in a different habitat than the other species (Fig. 4.5e).

As prey abundance declines, the models predicted species should fall out of assemblies in a regular order starting with Shovelers, then Wigeon, Gadwalls, Pintails and finally Mallards (Fig. 4.6). This order predicts assemblies should become more similar in morphological traits relevant to resource use.

Energetic rates were predicted to be sensitive to extreme values of prey size variability only (Fig. 4.7). However, the order in which species were predicted to fall out of assemblies lead to increasing morphological differences among species in some morphological traits (body mass and lamellar spacing), but not others (bill length).

4.5 Discussion

The foraging models clearly predict that all seven species of dabbling ducks face a trade-off between prey size selection and filtration rate. When feeding in environments that contain prey and detritus, dabbling ducks should ingest particles in the size classes that maximizes the proportion of prey ingested while maximizing filtration rates. Bill morphology interacts with the trade-off to determine the specific size range of particles each species can filter at the highest rate, leading to interspecific partitioning of prey by size. In the absence of detritus, species use a wide range of prey sizes, and tend to maximize net energetic rate when foraging on prey of the same size. If the size ranges of prey and detritus are equal, as the proportion of prey in the environment (Δ_P) decreases relative to the proportion of detritus (Δ_D), the net energetic rates of all species will decline, along with the overlap between realized niches. The interaction between morphology, the environment and resource use is a necessary piece of evidence supporting the case that dabbling ducks represent an adaptive radiation.

The link between bill morphology and prey size selection is easy to illustrate, particularly when comparing Gadwalls to Pintails. Consider the performance surfaces of Gadwalls and Pintails (Fig. 4.1). To maximize particle intake rate, individuals should use bill positions that keep them on the ridge of maximum filtration rate. To ingest a narrow size range of prey, individuals should use bill positions that minimize the difference between gape and lamellar separation. These positions will fall close to a line of maximum selection, which is drawn along the bottom plane of Figure 1 starting at the origin and with a slope of 1. Each species' ridge of maximum filtration rate runs parallel to the lamellar separation axis and they all cross the line of maximum selection. The ridge of maximum filtration rate for Gadwalls is closer to the lamellar separation axis than the Pintail ridge, and will cross the line of maximum selection at values of gape and lamellar separation that are lower than the values for Pintails. Consequently, Gadwalls should prefer to select smaller prey than Pintails. The ridge of maximum filtration rate for the Shoveler exists furthest from the lamellar separation axis, yet they prefer to select the smallest prey of all seven species. This apparent inconsistency is explained by the fact that increasing lamellar separation causes a greater decline in filtration rate than decreasing gape (Fig. 1f), due to their long lamellae. Therefore, Shovelers achieve the greatest filtration rate, and maximum selection, at the smallest values of gape and lamellar separation.

The model predictions also confirm earlier speculation (Chapter 3) that dabbling ducks should share preferences for habitats with high Δ_P/Δ_D ratios and large differences in the mean size of prey and detritus, but have distinct preferences for prey of different size. Communities of

species that share a preferences for habitats based on primary characteristics, but have distinct preferences for habitats based on secondary characteristics, should show high niche overlap when resource concentration is high, or competitor densities are low, and increasing niche divergence as resources are depleted or competitor density increases (Rosenzweig and Abramsky 1986). Rosenzweig and Abramsky (1986) referred to this pattern as centrifugal community organization. Guillemain et al. (2002) documented patterns of habitat selection among dabbling ducks consistent with centrifugal organization. In the winter, Mallards and Green-winged Teal initially filter large seeds from the benthos in shallow water. As seeds are depleted, Mallards switch to filtering seeds in deeper water, while Teal remain in the shallow water, but begin filtering smaller seeds. This observation is consistent with expectations from the foraging models, which predict Teal should experience a smaller decline in intake rate as prey size decreases compared to Mallards (Fig. 4.4).

The prediction that Blue-winged and Green-winged Teal could not achieve positive net energetic rates indicates a factor has been omitted from the models. The problem is likely related to the allometric models estimating gut size, energy expenditure or metabolizable energy, because negative energetic rates occurred even when foraging rates were not limiting energy intake. Some variation in gut volume or length is expected to be independent of body mass. When food is less abundant or of lower quality, ducks reduce their body mass while increasing gut length (Miller 1975; Paulus 1982) to bring energy intake into equilibrium with energy expenditure. The estimates of mass I used may have been too high given the amount of energy they can extract from prey. Corn has a higher metabolizable energy content than I used in the models, yet Mallards with a mass of 1.04 kg lost weight when fed corn ad lib under confined conditions (see also Loesch and Kaminski 1989; Miller 1975). Ducks may also increase the energy content of their diet by consuming different types of prey. In the winter, when ducks are primarily granivorous, wild ducks increase the energy content of their diet by consuming aquatic invertebrates, which have a high energy content and are highly digestible. The two Teal species had the smallest body mass and would be most sensitive to changes in digestibility and rates of energy expenditure (Bruinzeel et al. 1997). While these adjustments to the models may change the mean and variance of niches slightly, they are unlikely to change the general finding that bill morphology leads to interspecific resource partitioning, as all of these factors will increase net energetic rates of all seven species.

The models predict well-defined partitioning of prey among the four species with the longest bills while partitioning is less distinct among the three species with the shortest bills (Fig.

4.4). This is expected because bill length affects the scaling relationship between gape and lamellar separation. When bills are long, a unit change in gape forces a smaller change in lamellar separation than for short bills. Consequently, the performance surfaces of species with short bills occupy a smaller area of parameter space and constrain opportunities for variation in performance. However, bill length imposes a functional trade-off on a different foraging mode: pecking (Kooloos and Zweers 1991; Van Der Leeuw et al. 2003). Wigeon have higher intake rates than Mallards when pecking, but the opposite is true when filter-feeding (Van Der Leeuw et al. 2003). In the summer (Krapu and Reinecke 1992) and especially the winter (Eerden 1984; Sutherland and Allport 1994) Wigeon consume more plant material than other dabbling ducks. While Teal are not grazers, they may be more efficient at exploiting aquatic resources by pecking than ducks with longer bills.

Whatever the foraging strategy used by Green-winged Teal, it must be efficient. As duck diversity decreases with north latitude, the species most commonly observed are Mallards and Green-winged Teal (Elmberg et al. 1997; Nummi et al. 1995). It is not surprising that Mallards are widely distributed. Mallards achieved the highest net energetic rate in every simulation, except when prey concentration was very low and detritus was absent.

The models did not provide any support for the predictions that species should select habitats on the basis of mean prey size or that declines in prey abundance would limit assemblages to species with the most divergent morphological traits. The simulations did not assess many combinations of prey and detritus size-frequency distributions, so I can not tell if these patterns will never be predicted by the models. I suspect some can, but only if more than one parameter describing the size-frequency distribution of particles varies along the gradient. Only the prediction that declines in prey size variation would lead to increasing morphological divergence of assemblages received support, but only when size diversity is very low. When the variation in prey size was decreased, the species that could maintain a positive net energetic rate over the widest range of prey sizes were able to persist in the community. Even this pattern was sensitive to other parameters of the particle distributions. If detritus concentration or mean prey size had been greater in the simulation, Shovelers would have dropped out of the community, and morphological variation would have decreased further. The important point is that the patterns predicted by earlier studies are not general and their absence should not be taken as evidence that bill morphology does not influence habitat choice or interspecific competition.

The conflicting results of earlier studies on the role of bill morphology in resource partitioning appear to have been caused by incorrect assumptions that gave rise to incorrect

predictions. In addition, earlier studies used patterns in species abundances to make inferences about competition and resource partitioning. These inferences can not be made from patterns of abundance (Schluter 1984), particularly if community organization is centrifugal. Although the interpretations of the patterns between bill morphology and habitat use documented by earlier studies are problematic, the variation in the patterns they documented may be robust (Nudds et al. 2000). The models suggest two explanations for this variation. First, the size-frequency distribution of prey or detritus may have varied between studies, both within and between habitats. Indeed, Nudds et al. (2000) suggested biases in wetland shape between studies may have affected the spatial distribution of prey. Future work should quantify the size-frequency distribution of prey and detritus in each habitat. Second, studies were conducted at different latitudes and ranged from regions with low density and diversity to regions with high density and diversity. The centrifugal model predicts that habitat selection will be influenced by the type and density of competitors, so some variation in habitat use is expected.

Table 4-1 Comparison of morphological characteristics of seven species of dabbling ducks. Mean values for body mass and lamellar density were taken from Nudds et al. (1994). See methods for a description of how the other values were derived.

Species	Mean body mass (kg)	Mean lamellar density (no./cm)	Maxilla length (mm)	Mean lamellar spacing (mm)	Maximum lingual retraction (mm)	Maximum lingual elevation (mm)
Mallard	1.18	8	55.0	0.5	12.5	6.00
Northern Pintail	0.95	10.1	57.8	0.375	11.8	5.69
Gadwall	0.9	12.2	50.0	0.25	10.2	4.92
American Wigeon	0.79	11.0	40.0	0.25	8.2	3.93
Northern Shoveler	0.66	21.5	70.0	0.125	18	6.00
Blue-winged Teal	0.42	12.2	43.0	0.125	8.8	4.23
Green-winged Teal	0.32	13.3	36.5	0.125	7.5	3.59

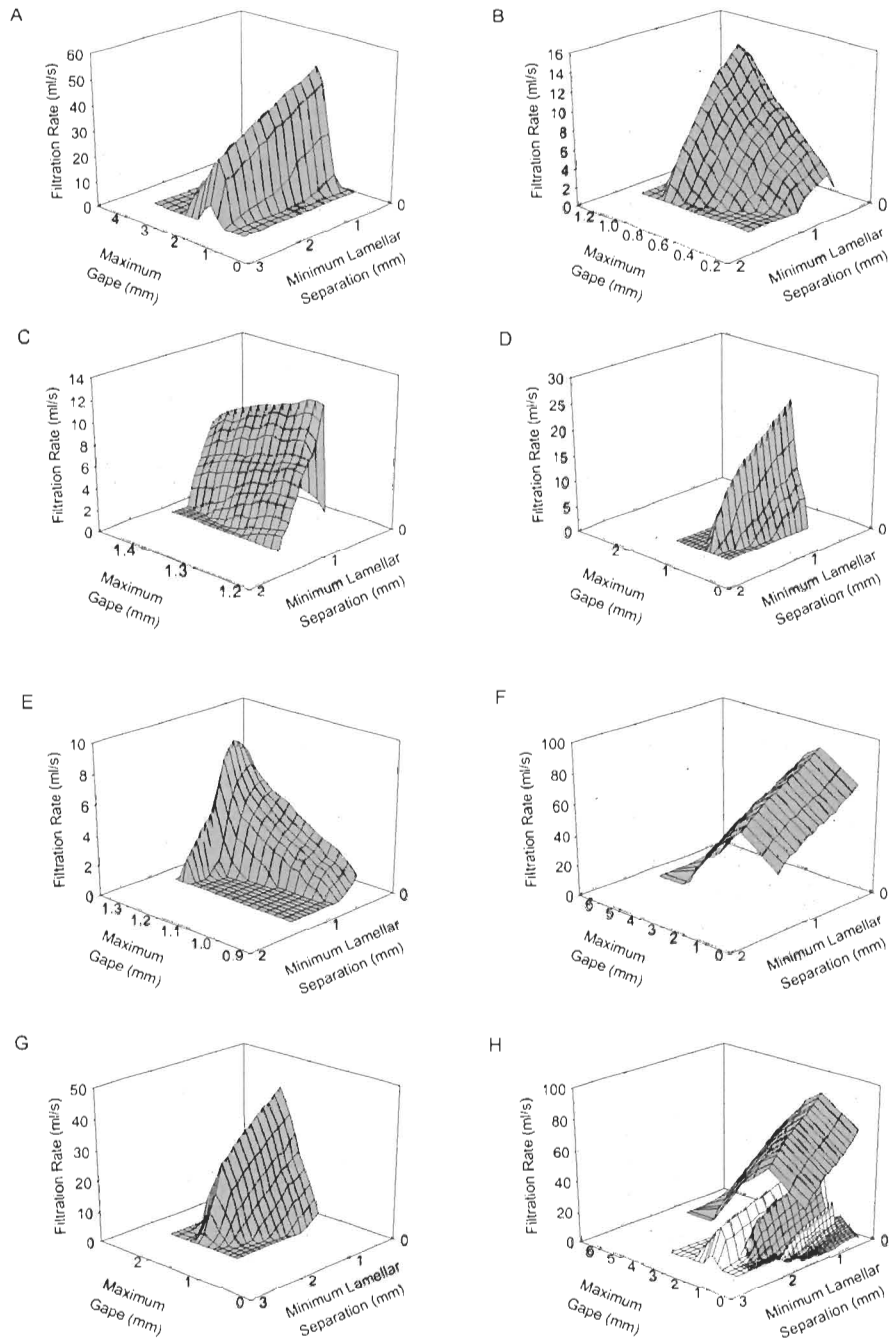
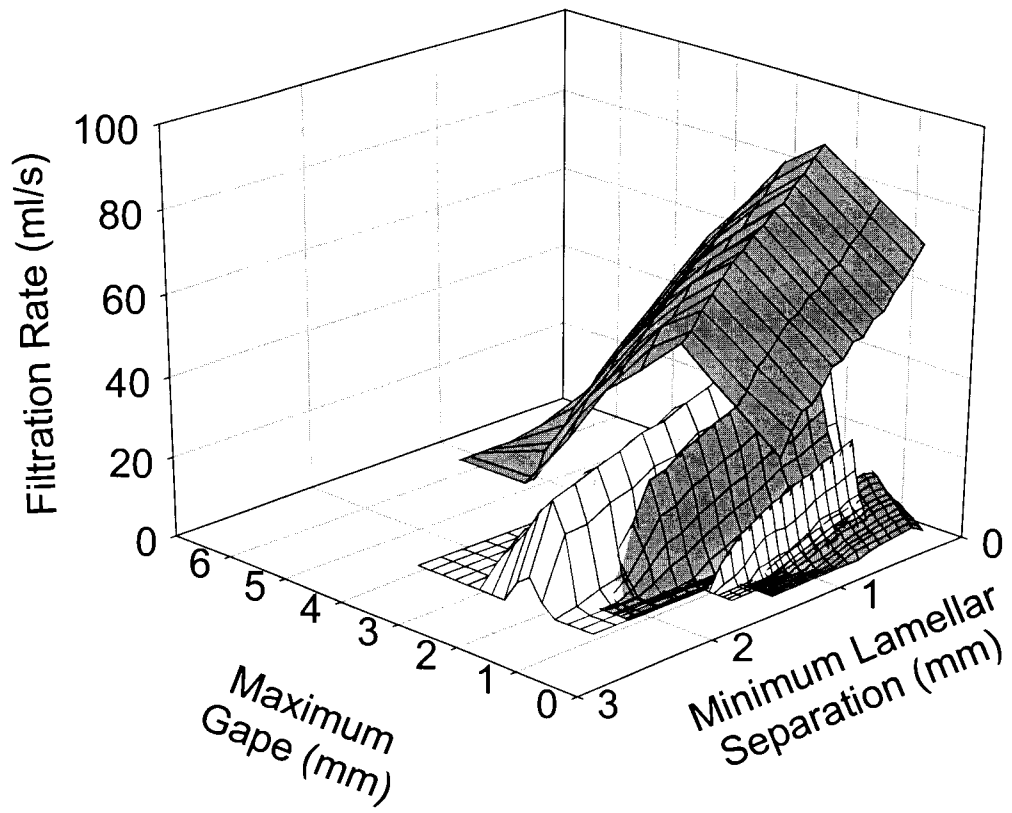


Figure 4-1 Combinations of gape, lamellar separation and water filtration rate that can be attained by Northern Pintail (A), American Wigeon (B), Blue-winged Teal (C), Gadwall (D), Green-winged Teal (E), Northern Shoveler (F), Mallard (G), and all species combined (H; enlarged on the next page). The two Teal species are unable to attain filtration rates greater than all other species at any combination of gape and lamellar separation and are not visible in Figure H. Note that the scale of the axes differs among Figures.



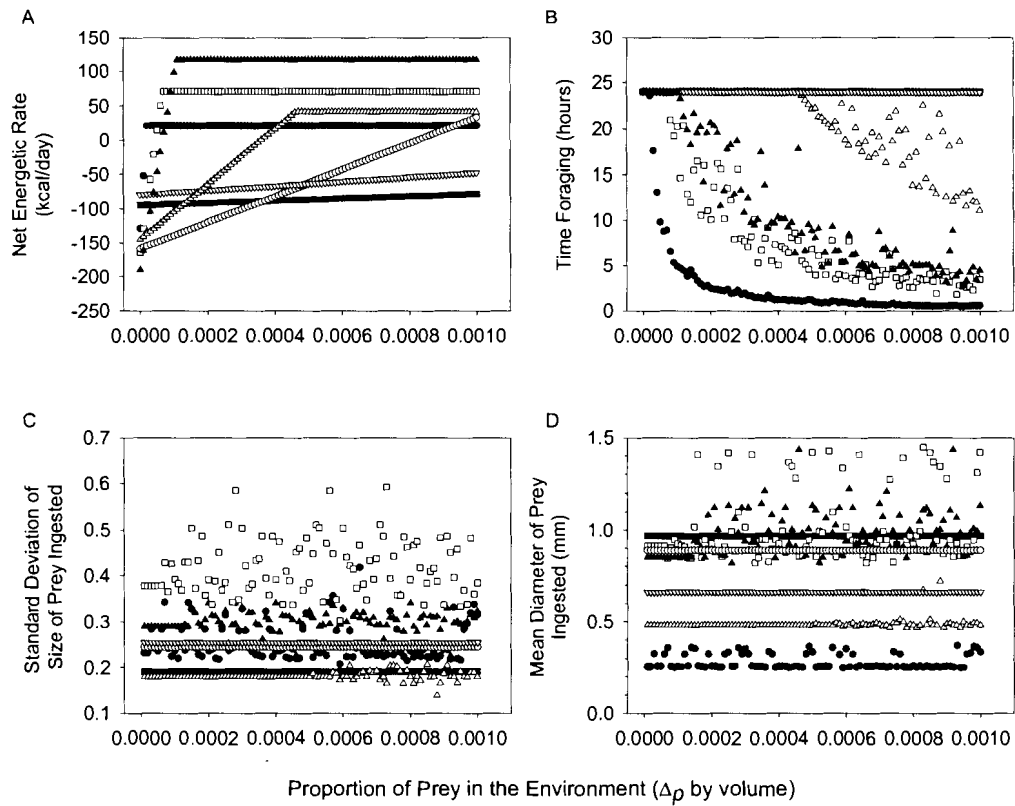


Figure 4-2 Predicted effect of the proportion (by volume) of prey in the environment ($\Delta\rho$) on net energetic rates (a), time foraging (b), the standard deviation of ingested prey size (c) and the mean size of ingested prey (d) by seven species of dabbling ducks filter-feeding in the absence of detritus. Prey were available in all size classes. Upright open triangles American Wigeon; open circles Gadwall; open squares Northern Pintail; upright closed triangles Mallard; closed circles Northern Shoveler; closed squares Blue-winged Teal; inverted open triangles Green-winged Teal.

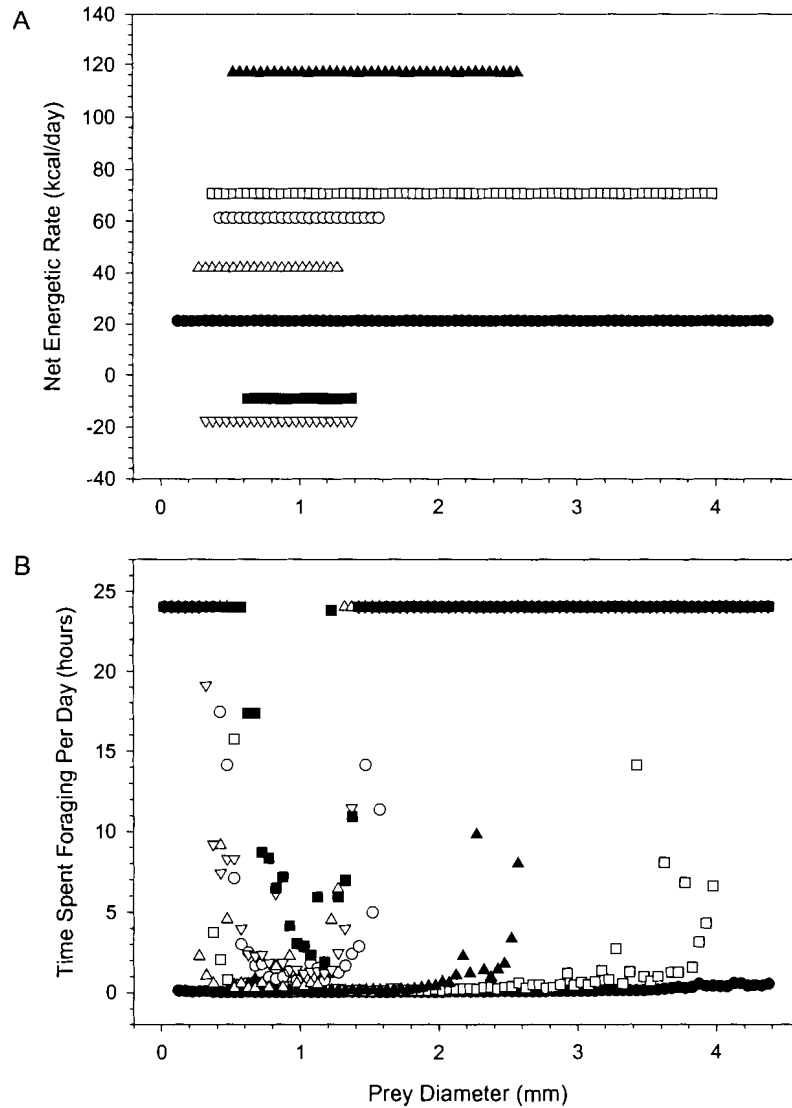


Figure 4-3 Predicted effect of prey size on net energetic rates (a) and foraging time (b) of seven species of dabbling ducks filter-feeding in the absence of detritus. Intake rates are either maximums or minimums. Only maximums are shown in (a). Prey were available in all size classes and the proportion of prey in the environment (Δ_p) was 0.006. Symbols as in Figure 4.2.

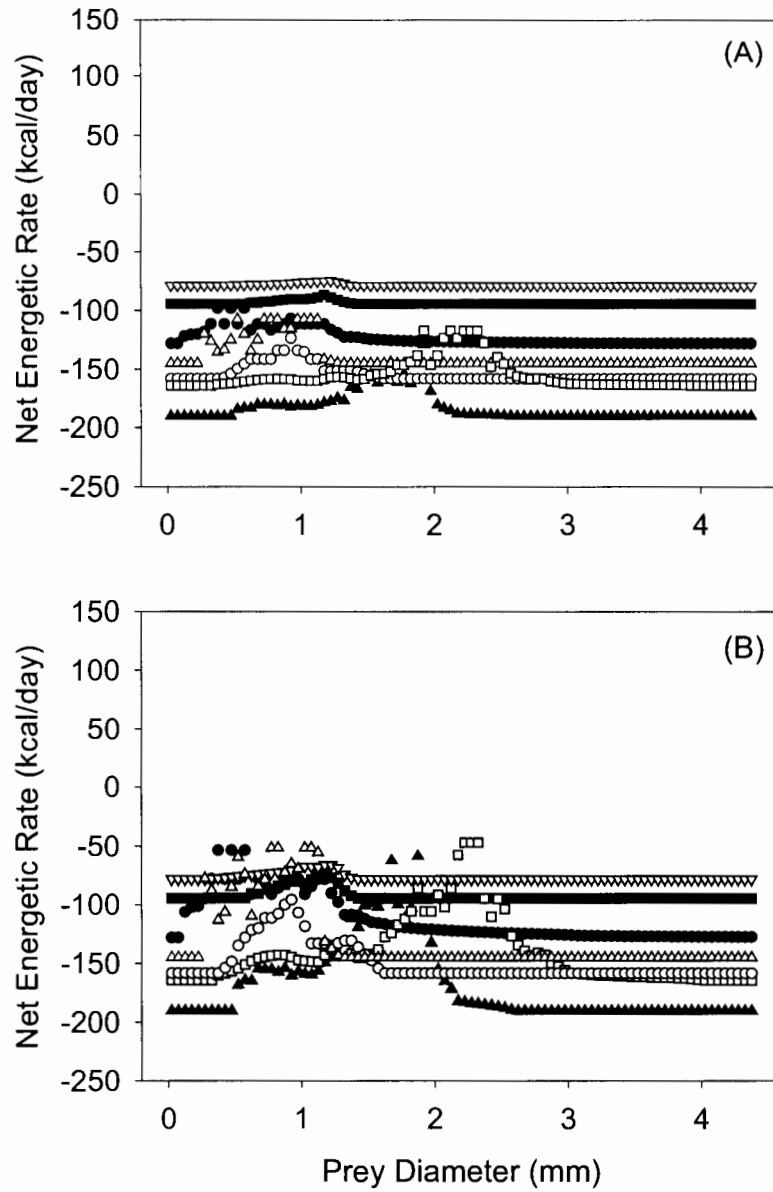
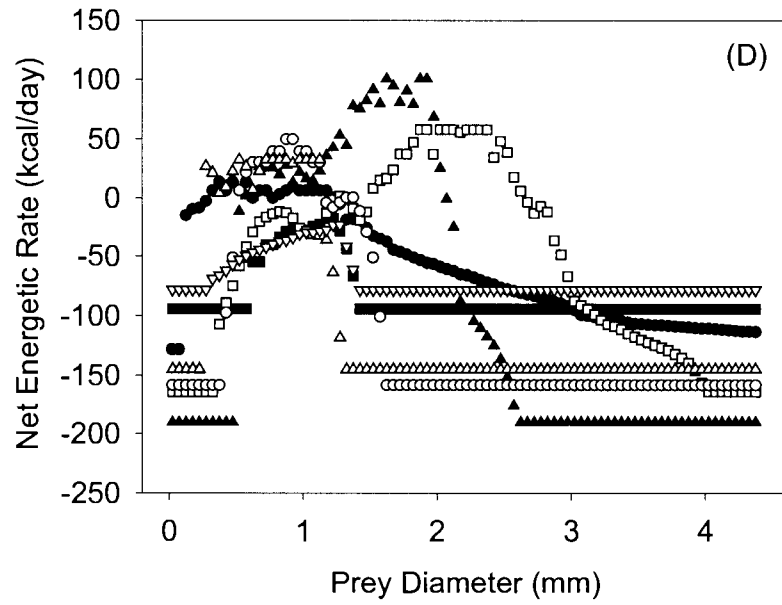
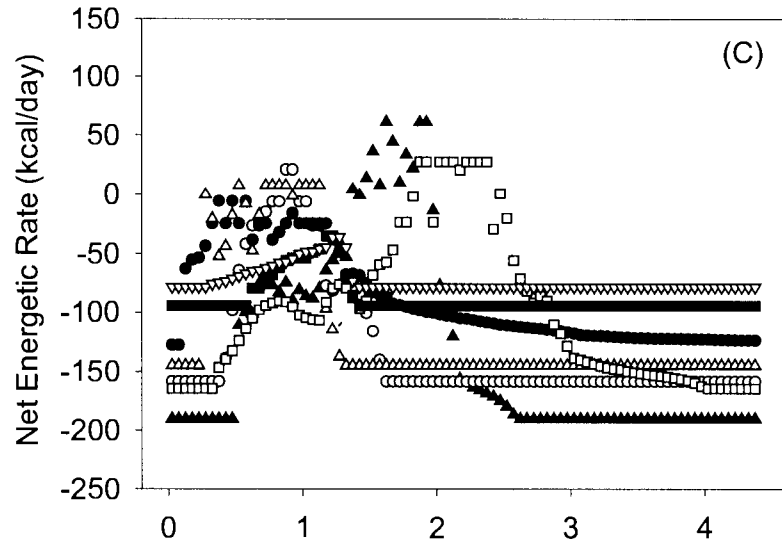


Figure 4-4 Next two pages. Expected net energetic rates of seven species of filter-feeding dabbling ducks foraging in different environments. Environments differ in the size of prey available (x-axis), prey concentration (A, B $\Delta_p=0.001$; C, D $\Delta_p = 0.018$) and detritus concentration (A, C $\Delta_D = 0.352$; B, D $\Delta_D = 0.088$). Species symbols as in Figure 4.2.



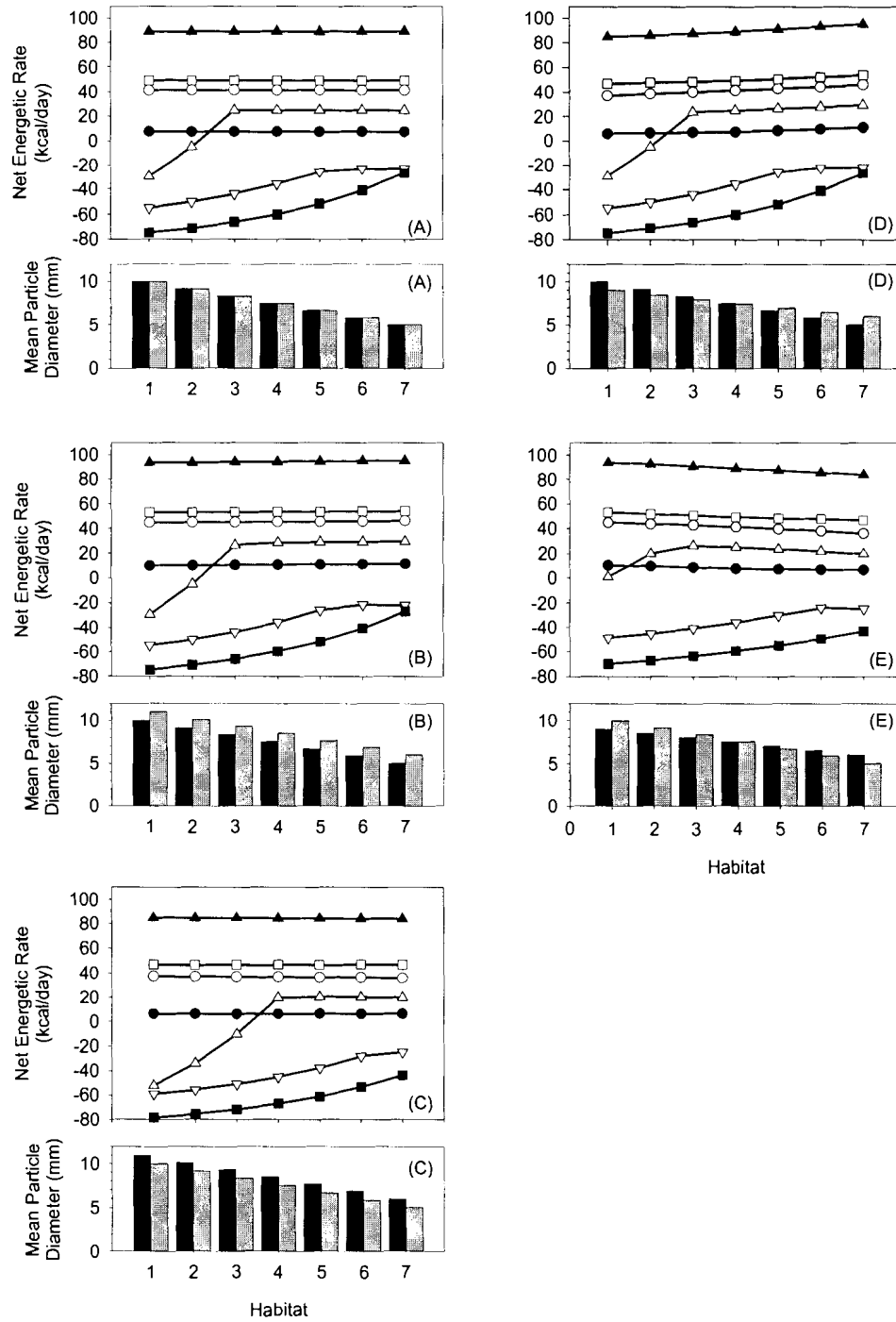


Figure 4-5 Expected net energetic rates of seven species of filter-feeding dabbling ducks foraging in seven habitats that differ in mean size of prey (dark bars) and detritus (gray bars). Species symbols as in Figure 4.2.

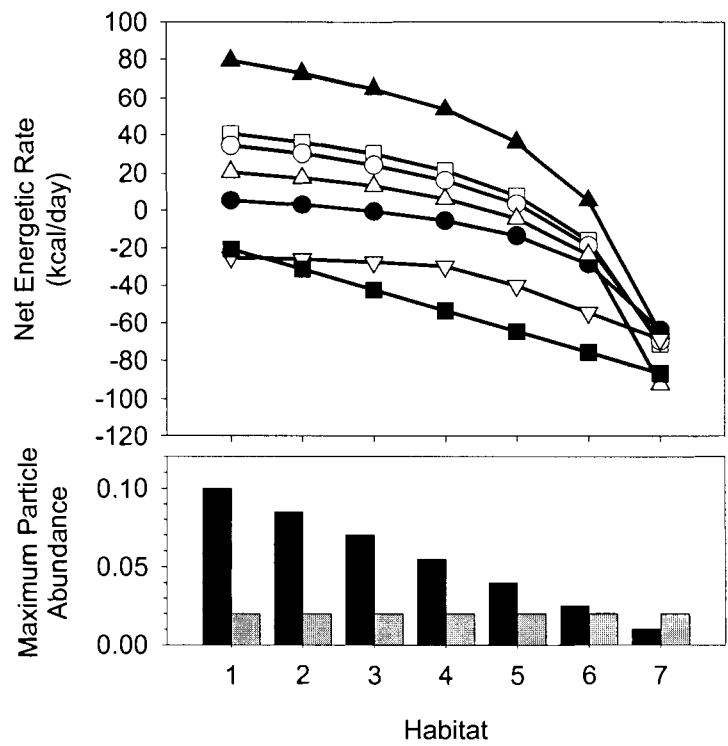


Figure 4-6 Expected net energetic rates of seven species of filter-feeding dabbling ducks foraging in seven habitats that differ in mean abundance of prey (dark bars) and detritus (gray bars). Species symbols as in Figure 4.2.

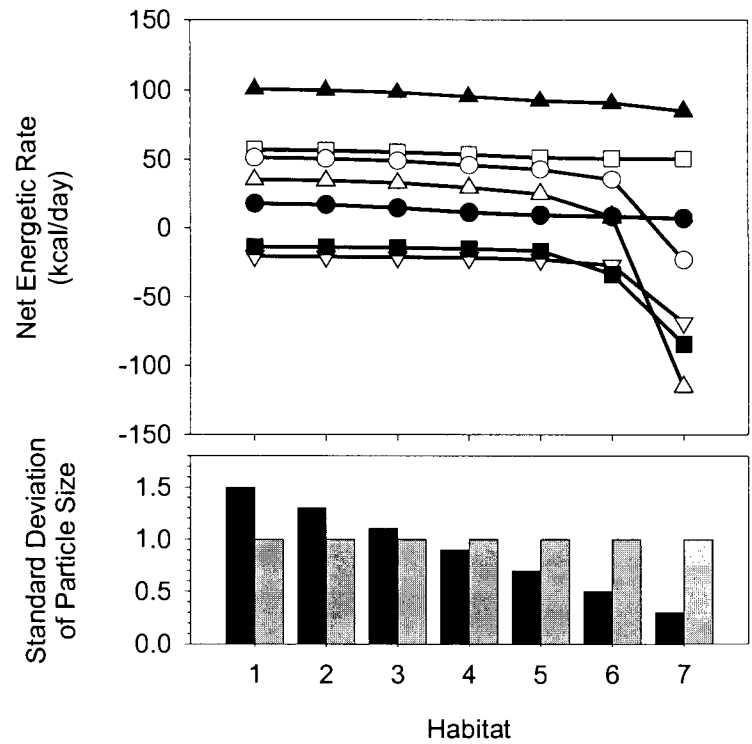


Figure 4-7 Expected net energetic rates of seven species of filter-feeding dabbling ducks foraging in seven habitats that differ in the variation in size of prey (dark bars) and detritus (gray bars). Mean prey size is 2.5mm. Species symbols as in Figure 4.2.

CHAPTER 5

INTERSPECIFIC AGGRESSION, PHENOTYPIC DIVERGENCE AND THE ORGANIZATION OF WATERFOWL COMMUNITIES

5.1 Abstract

The ecological theory of adaptive radiation proposes that divergent selection on phenotypic traits is the result of negative interactions between individuals that reduce fitness. Evidence that species interactions are negative, and that trait divergence reduces the fitness consequences of negative interactions, is most often lacking from tests of adaptive radiation. I used observed frequencies of aggressive, interspecific interactions among breeding waterfowl (Anatidae) and American Coots (*Fulica americana*) to test putative cases of phenotypic divergence: prey size partitioning through differences in bill morphology, vertical habitat partitioning through differences in body length and temporal partitioning through differences in nest initiation chronology. Culmen length, lamellar density, body mass and phylogenetic distance were also included in analyses. Observed frequencies of aggression between species pairs was compared to a null distribution expected if aggression was only a function of differences in species' relative abundance. Comparisons indicated waterfowl form two relatively independent guilds: (i) surface-feeding (dabbling) ducks (*Anas* spp.) and Coots and (ii) diving ducks (*Aythya*, *Bucephala*, *Oxyura* spp.). Intraguild aggression among divers was much more frequent than among dabblers. Differences in body length, body mass, lamellar density and prey size, all traits that reflect use of foraging resources, were negatively correlated with the frequency of aggressive interactions among dabblers, even after controlling for phylogenetic distance. Variation in aggression explained by phenotypic traits and phylogenetic distance was additive, indicating ecology and evolutionary history contribute independently to mechanisms influencing aggression. In general, each species of dabbling duck was aggressive to only two other species, consistent with niche partitioning along a single resource axis, such as size. Aggression among divers, which diverged earlier than dabbling ducks, was not correlated with phylogenetic distance or any of the other traits. Aggression was hierarchical and associated with nest initiation chronology in a non-linear fashion. Diving ducks may use aggression to cause other species to delay nest initiation, leading to temporal resource partitioning. Predictions of alternative explanations that

assume the advantage of aggression is not related to similarity in resource use were rejected. Results are most consistent with the hypothesis that trait divergence among dabbling ducks was driven by interspecific resource competition, leading to morphologically mediated resource partitioning. In comparison, diving ducks, which diverged earlier, and demonstrate stronger, ecological interactions, partition resources behaviourally.

5.2 Introduction

The ecological theory of adaptive radiation (Schluter 2000) proposes that divergent selection on phenotypic traits is the result of negative interactions between individuals that reduce fitness (Doebeli 1996; Gotelli and Bossert 1991; Law et al. 1997; Milligan 1985; Roughgarden 1972; Slatkin 1980; Taper and Case 1985; Taper and Case 1992). Phenotypic divergence reduces the fitness consequences of negative interactions by allowing individuals to exploit alternate resources and may lead to speciation (Rundle et al. 2000; Schluter 2001). However, evidence that species interactions are negative, and that the strength of these interactions decrease with phenotypic divergence, is most often lacking from tests of adaptive radiation (Schluter 2000).

Studies of adaptive radiation have traditionally focussed on exploitative competition for shared resources (Schluter 2000), but other negative interactions may also promote phenotypic divergence, such as interference competition (Adams 2004), apparent competition due to species interactions via a shared predator (Abrams 2000; Brown and Vincent 1992; Doebeli and Dieckmann 2000; Holt 1977) or intra-guild predation (Holt and Polis 1997).

Direct interference competition is of particular interest because it can enhance selection for phenotypic divergence (Schluter 2000) and because of its potential to interact with exploitation competition. Interference can enhance phenotypic divergence in two ways. First, interference can increase density dependence, which will expand the range of resources used by a population (Grand 2002; Moody and Houston 1995). Second, interference will facilitate matching of phenotypes to resources and mating among similar phenotypes because individuals are most likely to win access to the resources they exploit most efficiently (Sutherland and Parker 1992). Interference is expected to be an alternative strategy to resource exploitation efficiency (Case and Gilpin 1974), but the two can be functionally related. Interference will be most beneficial when its cost to the initiator is low, its cost to the target is high, and the benefit, in terms of the resources the target did not consume, is high (Case and Gilpin 1974; Mikami and Kawata 2004). Consequently, the benefit of interference should decrease with increased divergence in traits associated with resource exploitation. Traits should be selected carefully

because interference may select for divergence in traits that increase the effectiveness of interference rather than reduce exploitation competition (Adams 2004).

Alternatively, interference may not be related to interspecific resource competition at all. Interspecific interference may be a by-product of selection for aggressive behaviour in intraspecific interactions, avoidance of hybridization, or as a response to apparent competition (Schluter 2000). These mechanisms do not predict the benefit of interspecific interference will decrease with divergence in phenotypic traits involved in resource exploitation. The lack of a negative relationship between interference and phenotypic divergence is not evidence of apparent competition, selection for intraspecific interference or non-adaptive radiation, but a negative relationship is consistent with the evolution of phenotypic divergence due to negative species interactions.

Divergence in a number of phenotypic traits have been suggested to lead to resource partitioning among dabbling ducks (*Anas* spp.), a putative adaptive radiation. While filter-feeding, dabbling ducks are able to separate prey from indigestible detritus by size. Variation in bill morphology mediates a trade-off between filtration rate and prey size selection, leading to interspecific partitioning of prey by size (Chapters 3 and 4). Body length constrains the depth at which ducks can forage while 'tipped-up', leading to vertical resource partitioning (Guillemain et al. 2002; Lack 1971; Lack 1974; Pöysä 1983a; Pöysä et al. 1994). However, there is no trade-off associated with foraging depth so it is not clear what advantage ducks with short bodies have over ducks with long bodies. The outcome of competitive interactions may be dependent on variation in body mass (Persson 1985; Schoener 1983), which is highly correlated with body length. Body mass, through its relationship with metabolic rate and gut volume, can lead to resource partitioning because it constrains the quantity and quality of food on which a species can persist (Bruinzeel et al. 1997; Peters 1983). Toft (1982) analyzed co-occurrence of female dabbling and diving ducks with broods and found evidence of interspecific competition related to overlap in habitat selection and breeding chronology. They suggested that competition for food between ducklings (see also Sjöberg et al. 2000) has led to divergence in timing of nest initiation and selection of brood habitat between species.

All of these putative cases of phenotypic divergence currently lack evidence linking negative interactions between species with phenotypic divergence (Chapter 1). I tested for negative relationships between frequencies of interspecific aggression and differences in species' mean phenotype among sympatric dabbling and diving ducks and American Coot (*Fulica americana*). Although two of the hypotheses are specific to dabbling ducks, I included diving

ducks and Coots as they are very similar ecologically and may interact negatively with dabbling ducks. In addition, because of differences in their foraging behaviour and habitat, some of the mechanisms of resource partitioning thought to underlie phenotypic divergence in dabbling ducks do not apply to diving ducks. Consequently, diving ducks can serve as a natural 'control' to separate effects specific to dabbling duck ecology from those that apply to waterfowl in general.

5.3 Methods

5.3.1 Aggressive Interactions

Data was collected from mid-April, immediately after all study ponds were free of ice, until early July 1998-2000 near Riske Creek, B.C. Ponds were small (<10 ha) and contained sparse emergent vegetation, allowing ducks to be observed easily. Observations were conducted from blinds for four hours starting at dawn. Observers spent an equal number of days at each pond to control for observer bias. As many aggressive interactions as possible were observed during the four-hour period (the first priority of observers was to record data for a related study on foraging).

Aggression in waterfowl is overt and consists of pursuit in the air and above and below the water surface. I recorded an uninterrupted pursuit of one individual after another as one interaction, regardless of the duration of the pursuit or whether it resulted in physical contact. Pursuits were considered interrupted if the individual initiating the pursuit (the aggressor) switched to another target (the victim) or discontinued the pursuit. At the end of each interaction the species and sex (when possible) of the aggressor and victim were recorded. All individuals visible on the pond were surveyed every half hour. In 1998 and 1999 12 ponds were included in the study; in 2000 only four were included. Observations were conducted 376 times, for a total of 1504 hours.

Fifteen species of waterfowl were included in the analyses: seven species in each of the diving and dabbling duck guilds and the American Coot (Table 5.1). Species were excluded from the analysis if they were observed fewer than 100 times during surveys. Observations involving females with broods were also excluded.

5.3.2 Phylogenetic Relationships

To control for the non-independence of cross-species data, I quantified the evolutionary relationships between species in each guild. I measured genetic distance between species of

diving ducks from a phylogeny (Fig. 5.1a) based on a 648 base-pair region of the mitochondrial gene cytochrome *c* oxidase 1 (C. Francis, unpublished data). I measured time since divergence from a phylogeny of dabbling ducks (Fig. 5.1b) based on 2147 base pairs from the coding region of the mitochondrial genes ND2 and cytochrome-*b* (Johnson and Sorenson 1998).

5.3.3 Phenotypic Traits

Species' mean values for the various phenotypic traits are given in Table 5.1. Means were taken from the literature whenever possible.

Timing of nesting by waterfowl varies temporally, spatially and interspecifically. Migration distance, local climate, adverse spring weather between years and length of the breeding season all affect nest initiation dates (Bellrose 1976; Greenwood et al. 1995). In spite of this variation, waterfowl exhibit regular and repeated spacing of relative nest initiation (laying of first egg) dates (Bellrose 1976; Greenwood et al. 1995; Hammond and Johnson 1984; Higgins et al. 1992; Keith 1961; Petrula 1994; Shutler et al. 1998; Stoudt 1971; Väisänen 1974) which reduces interspecific synchrony of the entire breeding cycle (Toft et al. 1982). Dabbling ducks initiate nests earlier, complete nesting earlier, and have shorter gaps between species' peak initiation dates than diving ducks (Bellrose 1976; Greenwood et al. 1995; Hammond and Johnson 1984; Higgins et al. 1992; Keith 1961; Petrula 1994; Stoudt 1971; Väisänen 1974). Cavity nesting diving ducks are an exception. In Riske Creek, Barrow's Goldeneye (*Bucephala islandica*) and Bufflehead (*B. albeola*) initiate nests at the same time as early-nesting dabbling ducks (Campbell et al. 1990).

To determine the nest initiation chronology of species, I collected published and unpublished data on nest initiation dates for waterfowl in the Riske Creek region as well as published data from other regions of North America (Table 5.1). Because data were not always available for all species in the same region during the same years, it was necessary to combine the available data together. I ranked the relevance of each study based on the number of species studied, the number of nests recorded, the number of years of data, type of data collected (actual nests or back-dating of broods) and latitudinal and climatological similarity to Riske Creek. Within each study, I ranked species by nest initiation chronology. To reduce the effect of re-nesting on the chronology, I used modal dates of first nests over means when possible. The data were very consistent and I found few contradictions, especially among highly ranked studies. However, few data were available for Cinnamon Teal (*A. cyanoptera*).

I used the model predictions from Chapter 4 to quantify divergence in prey size. For each species, I determined the size of prey each species is most efficient at separating from detritus. As long as detritus is present, these peaks in efficiency are insensitive to changes in prey or detritus concentration. I included culmen length and lamellar density in the analysis as well. Although these are only two of many traits that determine prey size partitioning among dabbling ducks, individual traits may be reasonable indexes of divergence of more complex phenotypes if scale consistently among species.

Due to incomplete data, some species were excluded from some analyses. Coots do not have lamellae and were not included in either phylogeny and biomechanical models have not been constructed for Cinnamon Teal. Consequently, some correlations between aggression and phenotypic divergence were calculated twice (with and without Cinnamon Teal) for the dabbling duck guild.

5.3.4 Testing for Interspecific Differences in Frequencies of Aggression

I used a null model approach (Gotelli and Graves 1996) to test if the frequency of aggression differs between species pairs. Even if the strength of ecological interactions are the same among all species, aggression may vary simply because the relative abundance of species differ. I therefore used a null model to randomly sample the survey data and generate a null distribution of aggression frequencies assuming the strength of ecological interactions were equal between all species pairs. For each four-hour observation period, one of the nine surveys was chosen at random and an aggressor and victim were randomly chosen from the survey. The probability of a species being selected as an aggressor or victim was determined by each species' relative abundance. Selections were made with replacement, so that the same individual could be an aggressor or victim in repeated interactions, but not as both the aggressor and victim in the same interaction. Pairs of species were generated until the number of randomly generated interactions was equal to the number of interactions recorded during the observation period, which kept the total number of aggressive interactions in each null data set equal to the total number of observed interactions. Two hundred null data sets were generated.

To compare the observed and null data sets, I created contingency tables (aggressor species x victim species) and calculated the χ^2 test statistic for the observed data set and the two hundred null data sets. I then compared the χ^2 calculated from the observed data to the distribution of the two hundred χ^2 statistics generated from the null data sets. I repeated this analysis five times to test for differences in aggression frequencies at four levels: between species

at the community level (15x15 table), between diving and dabbling ducks at the guild level (2x2 table), and between species within each of the two guilds (7x7 tables). The analysis at the community level was conducted with, and without, intraspecific aggression, but this was excluded from analyses between and within guilds. I calculated z-scores to determine the probability that the observed χ^2 could have been drawn randomly from the distribution of null χ^2 values.

I used the expected frequency of aggression generated from the null model to standardize the observed frequencies of aggression. The standardized frequencies (θ_{ij}) are given by

$$\theta_{ij} = F_{ij} / C_{ij} N \quad 2$$

where F_{ij} is the observed frequency of aggression between aggressor species i and victim species j , C_{ij} is the probability of an interaction between species i and j under the null model, and N is the total number of aggressive interactions observed. All species co-occurred on ponds so that all $C_{ij} > 0$. If $\theta_{ij} = 1$ species interact at the same frequency as expected from the null model. If $\theta_{ij} > 1$ species interact more frequently than expected and if $\theta_{ij} < 1$ they interact less frequently than expected. To test if values of θ_{ij} for each interaction were different from 1, I calculated z-scores to determine the probability that the value of F_{ij} could have been drawn at random from the distribution of values of $C_{ij} N$ generated by the null model.

I used least-squares regression to estimate the correlation between θ_{ij} and phenotypic divergence in the characters hypothesized to function in resource partitioning. To account for the non-independence of multiple contrasts between species, I generated R^2 statistics and P values of the regression coefficients using a multiple regression extension of the Mantel permutation test (Legendre et al. 1994). The test assumes the dependent variable θ_{ij} represents a matrix of distance metrics that possess the properties of symmetry, non-negativity and definiteness and obeys the triangle inequality. The θ_{ij} matrix was not symmetric (i.e. $\theta_{1,2} \neq \theta_{2,1}$) for six interactions between dabbling ducks and 15 interactions between diving ducks, so I excluded the smallest value of θ_{ij} for each species pair from the matrix. When species interactions are not symmetric, the more efficient species is expected to be less aggressive, leading to an under-estimation of the degree of ecological similarity. Excluding small values also maximized the amount of variation available to be partitioned by phenotypic divergence. The matrix did not meet the property of distinctness (i.e. the distance between species i and j is zero if, and only if, $i = j$). Transformation of θ_{ij} to meet the distinctness property had no effect on the results except to change the sign of the correlations, so I only report results for untransformed values of θ_{ij} . To determine whether phenotypic divergence can account for variation in aggression in addition to phylogenetic

distance, I conducted regressions with and without phylogenetic distance as a second, independent variable. Statistical tests of correlations were based on 10000 permutations. Copies of software for conducting multiple regression Mantel tests are available at www.bio.umontreal.ca/Casgrain/en/labo/permute/.

5.4 Results

A total of 2181 aggressive interactions were observed. As expected, intraspecific aggression was more frequent than interspecific aggression (1415 observations compared to 776). In all five comparisons the χ^2 statistic calculated from the observed data set was significantly different from the χ^2 statistic calculated from the 200 null data sets (Fig. 5.2). Intraspecific aggression was more frequent than expected, while interspecific aggression, either between or within guilds, was less frequent than expected (Fig. 5.3a).

Variation in aggression at the guild level was striking. Diving ducks were more aggressive, both absolutely and relative to predictions of the null model, than dabbling ducks (Table 5.2). Interguild aggression was less frequent than expected, while aggression within the dabbling duck guild was similar to expectations. Coots were very aggressive. They initiated 397 intraspecific interactions and 269 interspecific interactions. Coots were aggressive towards dabbling ducks more frequently than expected, but aggression towards diving ducks was less frequent than expected (Fig. 5.3b). Coots were rarely victims of duck aggression (Fig. 5.3b). None of the estimates of θ_{ij} between Coots and diving ducks were significantly greater than 1. These results indicated weak interactions between the two guilds of ducks and stronger interactions between coots and dabbling ducks. Consequently, I excluded interguild aggression from the following analyses and included Coots as part of the dabbling duck guild.

Estimates of θ_{ij} varied within and between guilds. Within the diving duck guild, Barrow's Goldeneye and Bufflehead were the most aggressive and interacted with almost all other diving duck species (Table 5.3). Within the dabbling duck guild, Coots were the most aggressive and interacted with all dabbling duck species (Table 5.4). The pattern of aggressive interactions differed between the two guilds. Dabbling ducks tended to be aggressive towards 1-3 species, such that species could be arranged in a row (Fig. 5.4a), while diving ducks tended to be aggressive towards 0-6 species, forming a dominance hierarchy (Fig. 5.4b).

Variation in θ_{ij} among dabbling ducks was negatively correlated with differences in body mass, body length, and prey size, but not phylogenetic distance (Fig. 5.5; Table 5.5). These correlations remained significant when phylogenetic distance was included as a covariate.

Lamellar density was negatively correlated with θ_{ij} only when combined with phylogenetic distance. Remarkably the variation in θ_{ij} correlated with divergence in phenotype and phylogenetic distance were additive. The R^2 values for the two variable models were very close to the sum of the R^2 values for the single variable models.

Variation in θ_{ij} among diving ducks was not correlated with any of the phenotypic traits or with phylogenetic distance. Casual observation of the data revealed a tendency for early nesting species to be aggressive towards many species while later nesting species were mostly victims. Perhaps aggressive species can force other species to delay nesting until later in the season (Fig. 5.6), effectively leading to resource partitioning through time. If so, a dominance hierarchy would not be detected by linear correlation. This hypothesis makes three predictions: the (i) frequency and (ii) proportion of aggressive interactions initiated by a species should decline with nest initiation chronology and (iii) aggressive interactions should be directed towards species that nest later than the aggressor species. All three of these predictions were supported for the diving duck guild and rejected for the dabbling duck guild (Figs. 5.7 and 5.8). The observed relationships among the dabbling ducks were not different from those predicted by the null model, but were strongly divergent among the diving ducks (Fig. 5.9).

5.5 Discussion

The observed frequencies of aggressive interactions within and between guilds differed strongly from the frequencies expected from the null model, indicating species direct aggression towards selected victims. Dabbling ducks interacted more frequently if they were similar in body mass, body length, lamellar density or consumed similar sized prey. The decline in aggression with increasing divergence in lamellar density and prey size is consistent with a link between aggression with resource competition. Although the relationship between body size and aggression is not clear, it is specific to the dabbling duck guild, suggesting it may be related to resource use as well. The tendency for dabbling ducks to be aggressive towards two other species is consistent with niche partitioning along a single resource axis as predicted by the foraging models in Chapter 4.

The diving duck guild appears to be structured by different mechanisms than the dabbling duck guild. Interference among diving ducks was not linearly correlated with any phenotypic traits or even phylogenetic distance. Rather, aggression was hierarchical and related to nest initiation chronology, supporting Toft et al's (1982) conclusion that diving ducks partition resources through time.

I was unable to resolve whether body size contributes to resource partitioning through vertical habitat partitioning or through other mechanisms related to body mass. Neither body mass nor body length was correlated with aggression among diving ducks, while both were correlated among dabbling ducks. However, Coots, which are capable divers, were highly aggressive towards dabbling ducks, suggesting a role for mechanisms other than vertical habitat partitioning.

There was very little co-variation between phylogeny, phenotypic divergence and aggression among dabbling ducks. Additive variance is consistent with the idea that phenotypic divergence among dabbling ducks has evolved at a faster rate than expected from the phylogenetic distance between species, implying selection as the cause of divergence. If phenotypic divergence was due to drift rather than selection, it should be proportional to phylogenetic distance and phylogenetic distance and phenotypic divergence would account for the same component of variation in aggression. In contrast, aggression between diving ducks was not correlated with phylogenetic distance. Results may differ between the guilds because the diving duck lineages began to diverge earlier than dabbling ducks (Donne-Gousse et al. 2002), providing more time for ecological divergence to overcome similarities due to shared evolutionary history. Losos et al. (2003) also found a weak relationship between ecological similarity and phylogenetic distance among *Anolis* lizards. In spite of more time for divergence, and stronger ecological interactions between species, diving ducks appear to partition resources behaviourally, while dabbling ducks appear to have evolved morphologically-mediated resource partitioning.

These inferences are dependent on the assumption that the benefit of aggression to the aggressor is the increased availability of resources gained by displacing competitors. Confidence in the assumption is gained if alternative explanations can be rejected. There are four alternatives. First, aggression does not incur costs or provide benefits to the aggressor and is not under selection. This is an unlikely scenario, but it can be rejected because it predicts frequencies of interspecific aggression should be randomly distributed among species pairs. Second, the benefit of aggression to the aggressor is not dependent on displacement of the victim. For example, aggression may be a courtship ritual (Nuechterlein and Storer 1985a; Nuechterlein and Storer 1985b). This explanation can also be rejected because it predicts patterns of aggression should be random as well. If the benefit is not dependent on the response of the victim, then the identity of the victim is not critical either. Third, the benefit of aggression is dependent on the response of the victim, but the aggressor and victim do not share resources. Apparent

competition or aggression towards predators or avoidance of hybridization are the only scenarios that satisfy this explanation. However, ducks are not predators of other ducks, apparent competition does not predict a correlation between aggression and traits involved in resource use and avoidance of hybridization is not inconsistent with adaptive radiation.

My interpretation of the data assumes the fitness benefit of aggression is dependent on overlap in resource use between aggressors and victims. However, the decision to exclude a competitor should also account for the cost of aggression (Case and Gilpin 1974; Mikami and Kawata 2004). This cost will be a function of the direct cost of being aggressive and the relative fitness value of alternative habitats to the victim. If alternative habitats offer the same fitness, less aggression should be necessary to cause victims to switch habitats. The direct cost of defence is not likely to depend on the species of the victim, but the cost of switching habitats may vary substantially. However, the fitness value of alternative habitats will depend on environmental conditions and the population density of other species. Both of these factors will vary over time scales that may be too short for aggressors to track. Consequently, it is not unreasonable to expect that species select victims based on species identity, and thus resource overlap.

The time and energy invested in aggression should be related to the relative value of alternative habitats to the aggressor. The highest frequency of interspecific aggression was due to Coots interfering with dabbling ducks. Considerable evidence exists to support the assumption that the fitness of Coots is very sensitive to resource abundance. In a four-year study of 417 Coot pairs, 52 percent of chicks starved to death within 10 days of hatch (Lyon 1993). Because young are dependent on the adults for food soon after hatch, parental care limits the number of young fledged (Lyon 1993). Supplemental food increased brood survival and fledgling mass (Arnold 1994). Coots are also facultative intraspecific nest parasites, but have evolved the ability to identify parasitic eggs, which would only be favoured if brood size was limited (Lyon 2003). Finally, ornamental plumages of coot chicks appear to be the result of parents directing limited care to specific young (Lyon et al. 1994).

The two waterfowl guilds interacted weakly and appear to be structured by different mechanisms. Models of density-dependent habitat selection predict guilds of closely related species should be organized by either interference or exploitation competition (Case and Gilpin 1974; Pimm and Rosenzweig 1981; Rosenzweig 1979; 1981; 1987). Guilds organized by exploitation competition should be composed of combinations of specialist and generalist species that utilize different habitats (Brown 1990; Brown and Rosenzweig 1986; Rosenzweig 1979;

1981; 1987). Guilds organized by interference competition should be composed of specialist and generalist species that partition resources in space or time and exhibit a hierarchical system of dominance between species (Case and Gilpin 1974; Rosenzweig 1979; 1987). The patterns I detected seem to agree with these models. The dabbling duck guild was characterized by less frequent aggression and divergence in three phenotypic traits were negatively correlated with θ_{ij} , suggesting exploitation competition limited by morphology-mediated resource partitioning. In contrast, the diving duck guild was characterized by frequent aggression that was not associated with any of the phenotypic traits I considered. Dominance in the diving guild was hierarchical and appears to drive resource partitioning through time.

These results are consistent with the results of other studies of waterfowl community dynamics. Experimental increases in the density of Mallards had no effect on the density of Green-winged Teal (Elmberg et al. 1997), consistent with resource partitioning. Nudds (1983) analyzed 35 years of waterfowl census data for mixed-prairie and aspen-parkland habitats in central Canada. He found that in both habitats dabbling duck diversity increased only when total niche space increased, suggesting niches of dabbling ducks could not be compressed. In contrast, niche separation between species of diving ducks in aspen-parkland habitat was positively correlated with diversity, but not with total niche space. Niches of diving ducks appeared to compress, such that species of diving ducks segregated onto ponds with different characteristics when species diversity increased. Niches determined by behavioural responses to aggression should exhibit more overlap and allow species to adapt quickly to changes in resource availability and competitor density (Pimm et al. 1985; Rosenzweig 1986) compared to niches determined by fixed morphological traits.

Given the limitations of correlational analyses, these data are most consistent with the hypothesis that phenotypic divergence among diving and dabbling ducks is related to negative interspecific interactions as predicted by adaptive radiation. Divergent selection appears to have lead to morphologically mediated resource partitioning among dabbling ducks. In comparison, diving ducks, which diverged earlier, and demonstrate stronger, ecological interactions, partition resources behaviourally.

Table 5-1 Values of phenotypic traits potentially mediating competition between waterfowl species.

Species	Acronym	Body Mass (kg)	Body Length (cm) ^f	Culmen Length (cm)	Lamellar Density (cm ⁻¹)	Nesting Order ¹	Prey Size (mm)
Dabbling Guild							
American Wigeon (<i>Anas americana</i>)	AMWI	0.79 ^a	49.9	2.63 ^a	11.00 ^a	7	0.825
Blue-winged Teal (<i>A. discors</i>)	BWTE	0.42 ^a	38.0	2.10 ^a	12.18 ^a	5	1.175
Cinnamon Teal (<i>A. cyanoptera</i>)	CITE	0.39 ^b	40.0	3.36 ^c	12.18 ^c	2	na
Gadwall (<i>A. strepera</i>)	GADW	0.90 ^a	50.9	3.37 ^a	12.23 ^a	8	0.925
Green-winged Teal (<i>A. crecca</i>)	GWTE	0.32 ^a	36.3	2.78 ^a	13.28 ^a	6	1.275
Mallard (<i>A. platyrhynchos</i>)	MALL	1.18 ^a	60.7	4.05 ^a	7.96 ^a	1	1.725
Northern Shoveler (<i>A. clypeata</i>)	NSHO	0.66 ^a	48.4	4.80 ^a	21.48 ^a	3	0.475
American Coot (<i>Fulica americana</i>)	AMCO	0.52 ⁱ	34.7	2.00 ^h	na	4	
Diving Guild							
Barrow's Goldeneye (<i>Bucephala islandica</i>)	BAGO	0.86 ^g	46.0	3.53 ^g	8.50 ^h	1	na
Bufflehead (<i>B. albeola</i>)	BUFF	0.50 ^d	35.4	2.79 ^g	9.83 ^h	2	na
Canvasback (<i>Aythya valisineria</i>)	CANV	1.22 ^d	51.5	5.93 ^c	7.40 ^c	3	na
Lesser Scaup (<i>A. affinis</i>)	LESC	0.71 ^d	42.5	4.00 ^e	8.43 ^e	7	na
Redhead (<i>A. americana</i>)	REDH	1.03 ^d	49.5	4.60 ^e	7.42 ^e	4	na
Ring-Necked Duck (<i>A. collaris</i>)	RNDU	0.76 ^d	42.9	4.53 ^e	7.95 ^e	5	na
Ruddy Duck (<i>Oxyura jamaicensis</i>)	RUDU	0.54 ^f	38.7	4.03 ^e	9.53 ^e	6	na

^a Nudds and Bowlby 1984.

^b Palmer 1976.

^c Nudds and Kaminski 1984.

^d Barnes and Thomas 1987.

^e Kehoe and Thomas 1987.

^f Bellrose 1976.

^g Evans 2003

^h this study

ⁱ compiled from Keith 1961, Stoudt 1971, Livezey 1981, Toft et al. 1982, Hammond and Johnson 1984, Somerville 1985, Campbell et al. 1990, Lokemoen et al. 1990, Higgins et al. 1992, Gauthier 1993, Petrula 1994, Greenwood et al. 1995, Johnson 1995, DuBowoy 1996, Gammonley 1996, Kruse and Bowen 1996, LeSchack et al. 1997, Austin et al. 1998, Hohman et al. 1998, Shutler et al. 1998, Brua 1999, Mowbray 1999, Eadie et al. 2000, Brisbin et al. 2002, Brua 2002, Drilling et al. 2002, Mowbray 2002, Rohwer et al. 2002, Woodin et al. 2002.

^jLyon 2003

^kChapter 4

Table 5-2 Frequencies of aggressive interspecific interactions between guilds of dabbling and diving ducks. Expected frequencies were generated using a null model that accounted for differences in relative abundance of species. Both guilds contained seven species.

Aggressor	Victim			
	Dabblers		Divers	
	Observed	Expected Range	Observed	Expected Range
Dabblers	69	68-110	4	89-139
Divers	57	88-133	351	146-193

Table 5-3 Standardized frequencies (θ_{ij}) of interspecific and intraspecific aggression between species of diving ducks. Values significantly different from 1, which indicate species interact at a frequency different from the null expectation, are indicated with an asterix.

Aggressor	Victim						
	Barrow's Goldeneye	Bufflehead	Canvasback	Lesser Scaup	Redhead	Ring-necked Duck	Ruddy Duck
Barrow's Goldeneye	2.38*	6.57*	4.68*	1.97*	2.5*	0.6	0.27*
Bufflehead	4.58*	7.67*	1.31*	3.34*	0.97	5.86*	0.25*
Canvasback	0	0	4.03*	2.11*	5.07*	5.07*	0*
Lesser Scaup	0*	0.04*	0*	1.04	0*	0*	0*
Redhead	0*	0.32	0.46	0.28*	0.30*	0.30*	0*
Ring-necked Duck	0*	0*	0	0*	0*	0*	0
Ruddy Duck	0*	0*	0*	0.05*	0*	0*	2.05*

Table 5-4 Standardized frequencies (θ_{ij}) of interspecific and intraspecific aggression between species of dabbling ducks and Coots. Values significantly different from 1, which indicate species interact at a frequency different from the null expectation, are indicated with an asterix.

Aggressor	Victim							
	Coot	Wigeon	Blue-winged Teal	Cinnamon Teal	Gadwall	Green-winged Teal	Mallard	Shoveler
American Coot	3.23*	1.16	5.4*	6.8*	1.42	2.5*	2.55*	0.94
American Wigeon	0*	3.02*	0*	0*	1.59	0*	0*	0.55
Blue-winged Teal	0*	0*	2.17*	1.46	0*	0.61	0.61	0
Cinnamon Teal	0*	0*	1.09	3.69*	0	0*	0*	0
Gadwall	0	2.39*	0*	0*	10.99*	0.32	0.32	0
Green-winged Teal	0*	0*	0.24*	0*	0	0.87	0.87	0
Mallard	0.13*	0*	0*	0*	0.46	0.1*	0.1*	0
Northern Shoveler	0*	0.55	0.3	0	0	0	0	7.55*

Table 5-5 Statistics for the correlation between the standardized frequency of aggression (θ_{ij}) and phenotypic differences between species of dabbling ducks.

Group	Independent Variable	Independent variables alone			Independent variables with phylogenetic distance as a covariate		
		<i>r</i>	<i>P</i>	Model R^2	<i>r</i>	<i>P</i>	Model R^2
Including CITE	Body Mass	-0.52	0.001	0.27	-0.41	0.015	0.41
	Body Length	-0.54	0.001	0.29	-0.46	0.003	0.46
	Culmen Length	-0.02	0.508	0.0004	-0.18	0.18	0.28
	Lamellar Density	-0.24	0.095	0.06	-0.26	0.03	0.32
	Nesting Chronology	-0.25	0.154	0.06	-0.17	0.22	0.28
	Phylogenetic Distance	-0.5	0.036	0.25			
	Excluding CITE	Prey Size	-0.45	0.018	0.21	-0.43	0.019
	Phylogenetic Distance	-0.43	0.087	0.19			

Table 5-6 Statistics for the correlation between the standardized frequency of aggression (θ_{ij}) and phenotypic differences between species of diving ducks.

Independent Variable	Independent variables alone			Independent variables with phylogenetic distance as a covariate		
	<i>r</i>	<i>P</i>	Model R^2	<i>r</i>	<i>P</i>	Model R^2
Body Mass	-0.06	0.42	0.003	-0.06	0.42	0.04
Body Length	-0.006	0.50	0.000	0.01	0.47	0.04
Culmen Length	0.31	0.13	0.098	0.31	0.14	0.13
Lamellar Density	0.004	0.47	0.000	0.10	0.33	0.05
Nesting Chronology	-0.06	0.42	0.003	-0.02	0.48	0.04
Phylogenetic Distance	-0.19	0.26	0.037			

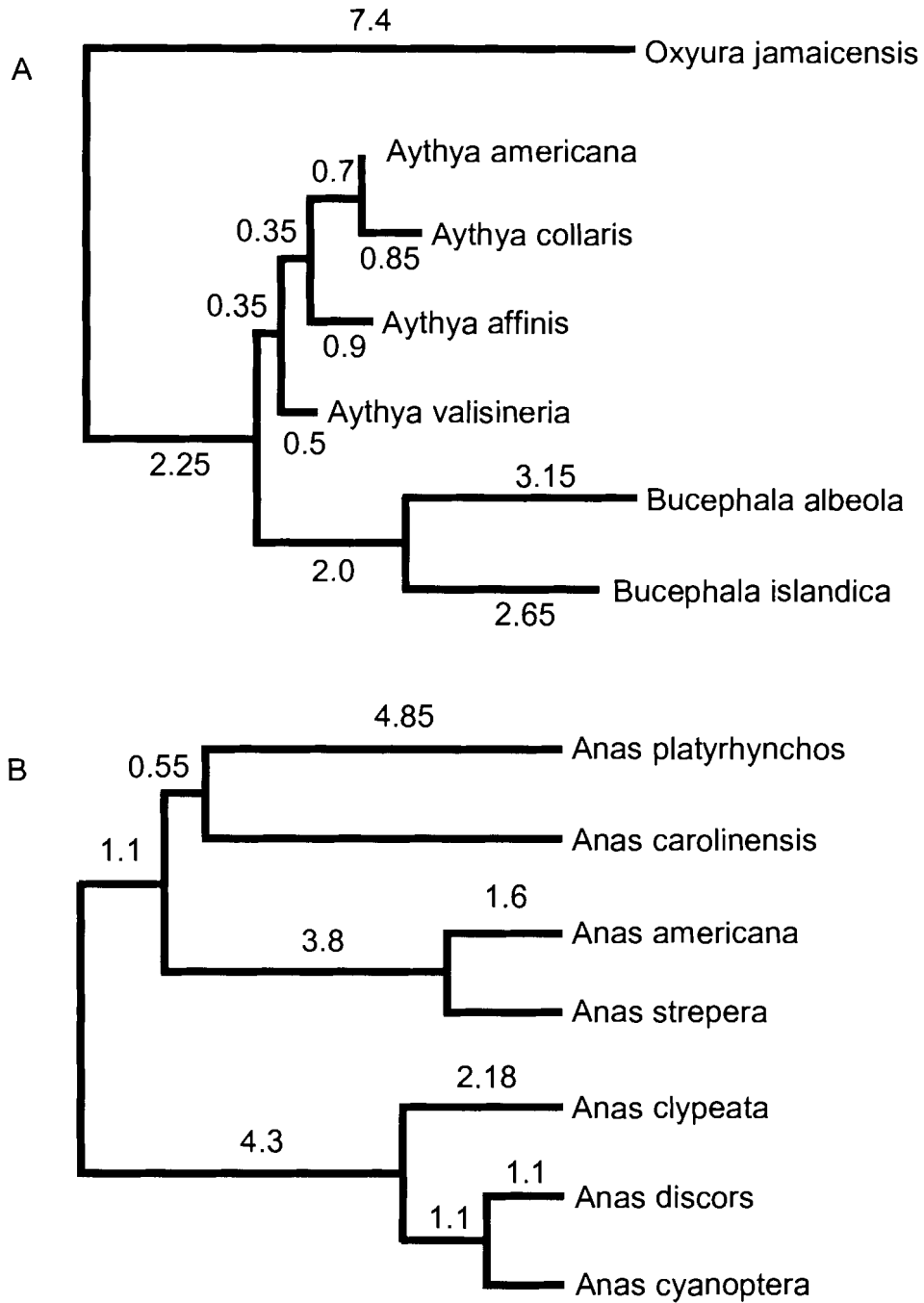


Figure 5-1 Phylogenetic relationships between select species of diving ducks (C. Francis, unpublished data) (A) and dabbling ducks (Johnson and Sorenson 1998) (B). Values above the branches give the branch length, which are proportional to the number of changes in the genetic sequence. Only partial trees are illustrated.

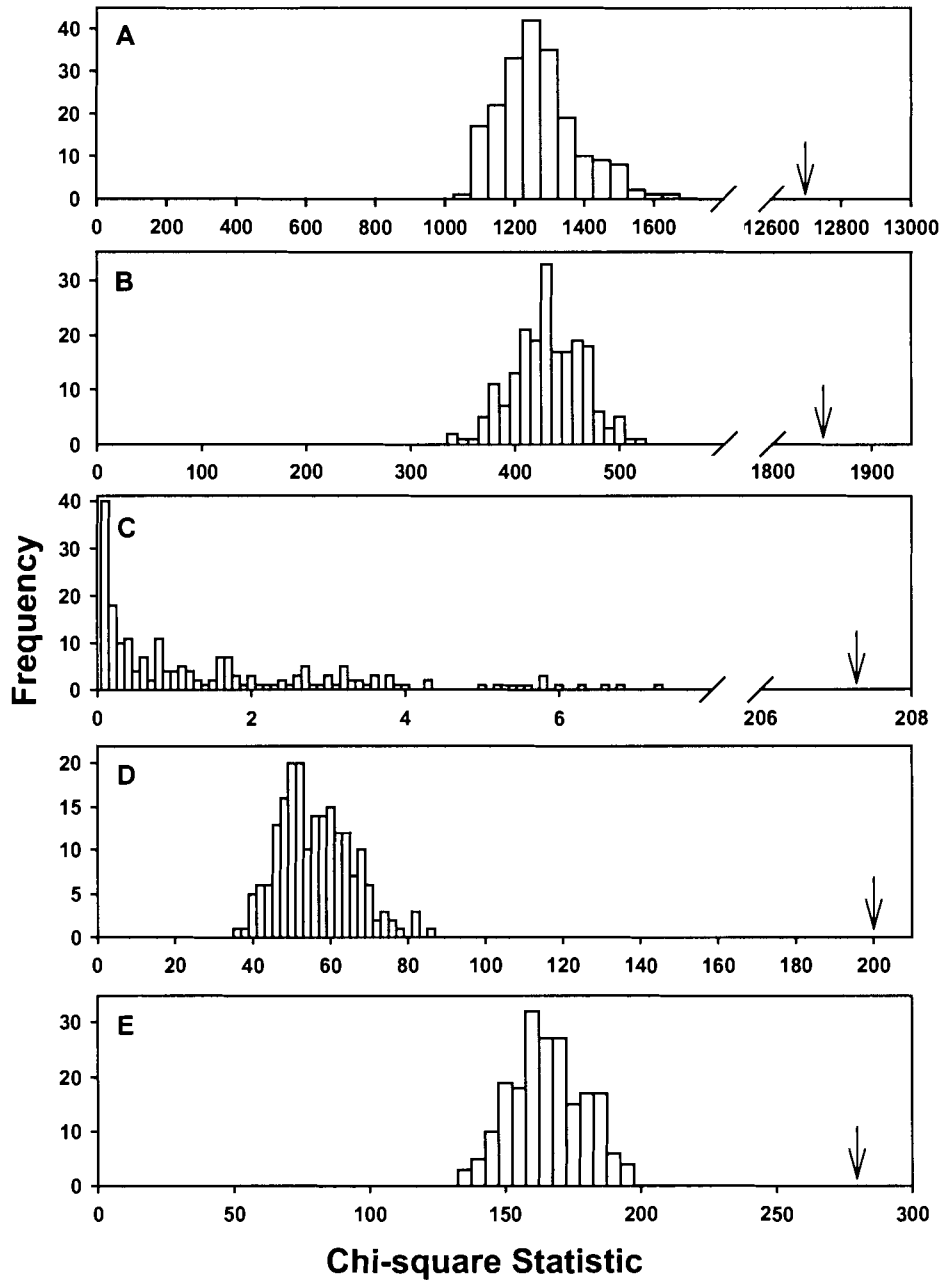


Figure 5-2 Tests for non-random patterns of interspecific aggression. Open bars indicate the expected X^2 values from 200 contingency tables generated by a null model that accounted for differences in species' relative abundance. Arrows indicate the observed X^2 values. (A) All species including intraspecific interactions. (B) All species excluding intraspecific interactions. (C) Between guilds. (D) Within the dabbling guild. (E) Within the diving guild. In each comparison the observed X^2 was outside the range of the expected distribution ($P < 0.005$).

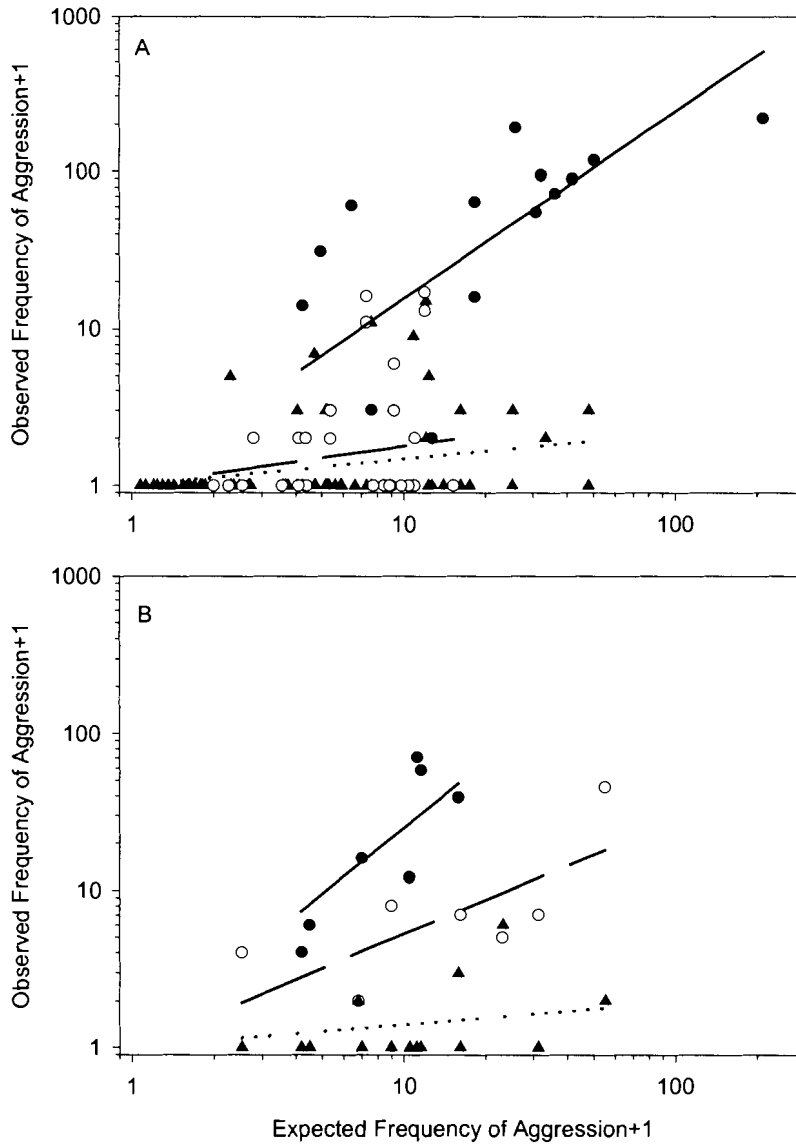


Figure 5-3 Comparison of observed and expected frequencies of aggression between diving and dabbling duck guilds. Points represent species pairs. Expected values were generated using a null model that accounted for differences in relative abundance. (A) Aggression between dabbling and diving ducks. Intraspecific aggression (solid circles, solid line) is more frequent than expected while intraguild (open circles, dashed line) and interguild (solid triangles, dotted line) aggression are less frequent. (B) Aggression involving Coots. Coots were more aggressive towards dabbling ducks (solid circles, solid line) than towards diving ducks (open circles, dashed line), but were rarely victims of aggression by ducks in either guild (solid triangles, dotted line).

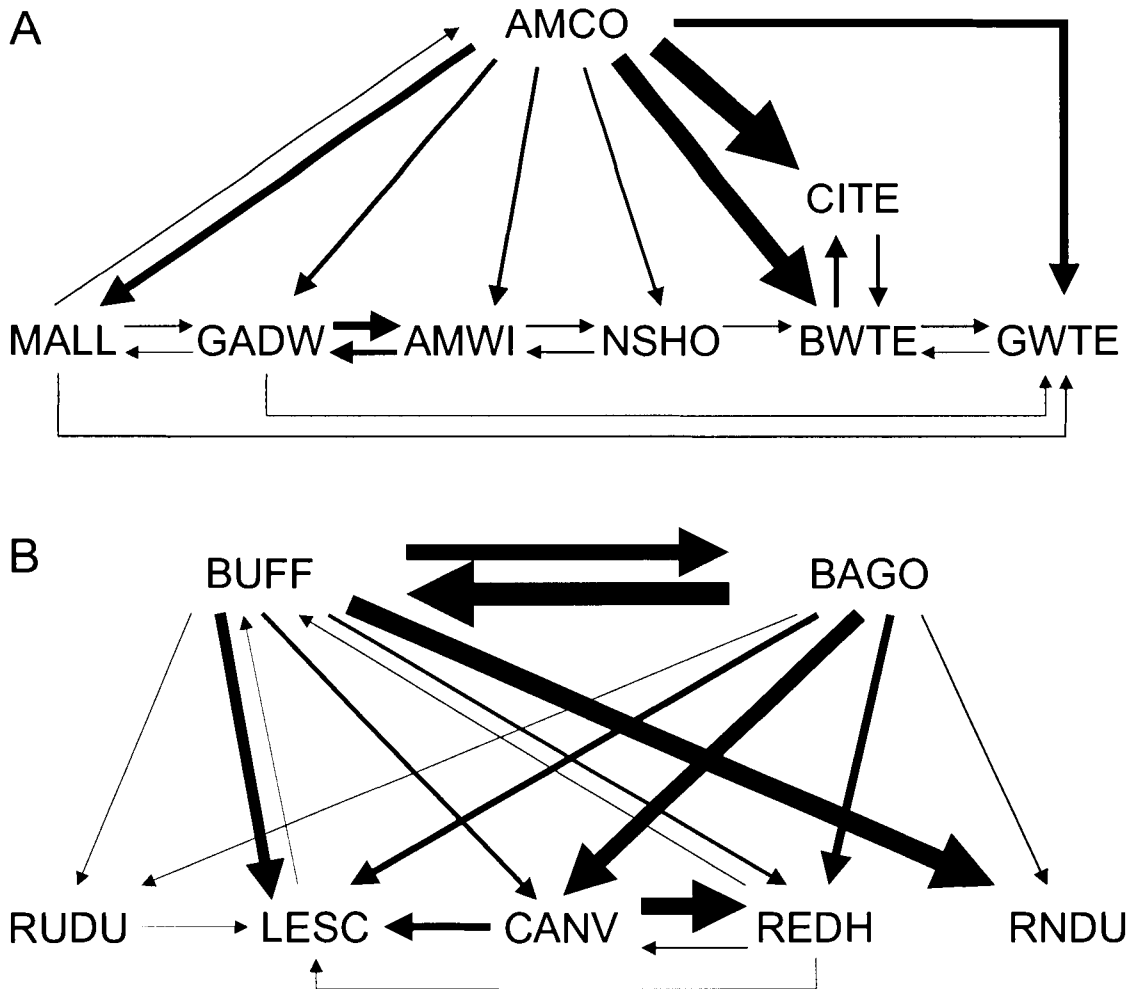


Figure 5-4 Direction and frequency of aggressive interspecific interactions between waterfowl. Arrows point from aggressor species to victim species and the thickness of the line is proportional to the standardized frequency of aggression (θ_{ij}). Species acronyms are given in Table 5.1. (A) Aggression between dabbling ducks and American Coots. (B) Aggression between diving ducks.

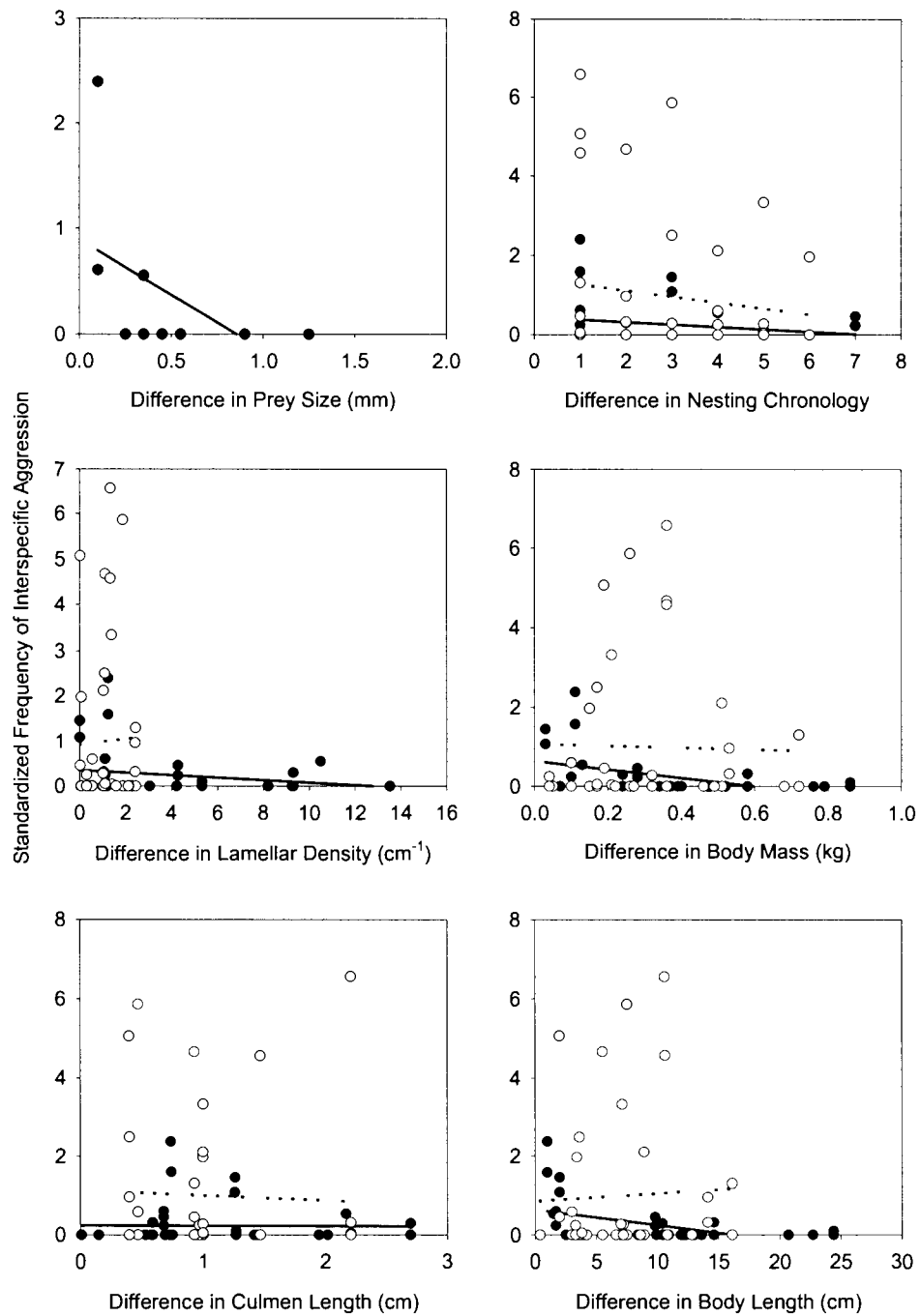


Figure 5-5 Regressions between the standardized frequency of aggression (θ_{ij}), and differences in phenotypic traits between species of diving ducks (open circles; dotted line) and dabbling ducks (solid circles; solid line). Each point represents a species pair. Statistics are given in Table 5.5 and 5.6.

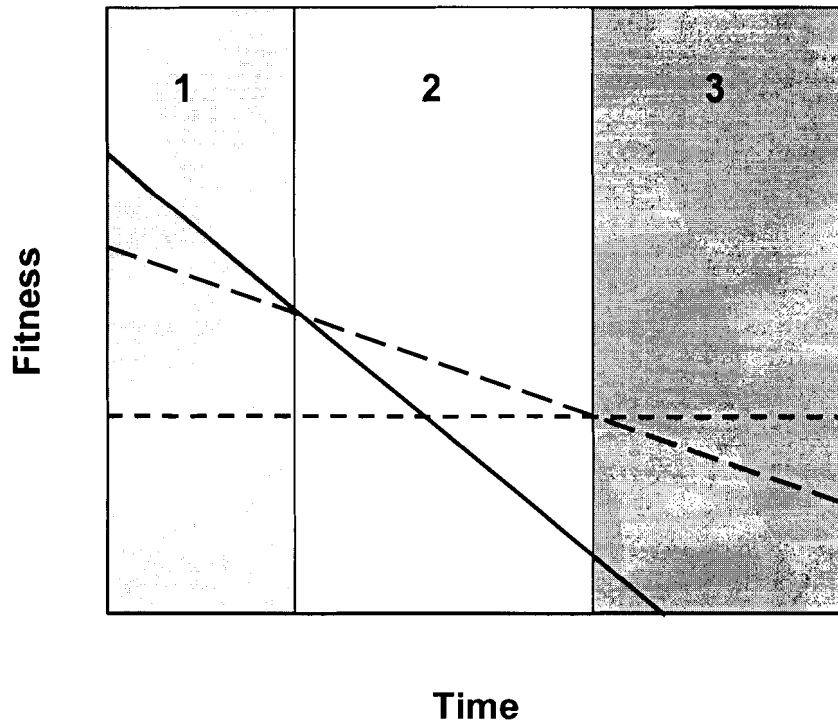


Figure 5-6 Aggressive interference could lead to resource partitioning through time. The fitness of three species A (solid line), B (dashed line), and C (dotted line) declines as nesting is delayed during the annual reproductive period. Each species has the highest fitness at one period of time. Species A is an early-nesting specialist compared to B, while C is a perfect generalist. I assume species exert density-dependent effects on each other and individuals can interfere with each other through aggressive interactions to delay breeding. If the fitness cost of aggression to the aggressor and the victim is equal for all species, then a steep slope means a greater investment in aggression can be made before fitness declines to the point that breeding should be delayed. A dominance hierarchy will result because species A could exclude B and C from period 1 and B could exclude C from period 2, leading to distinct nesting periods for each species.

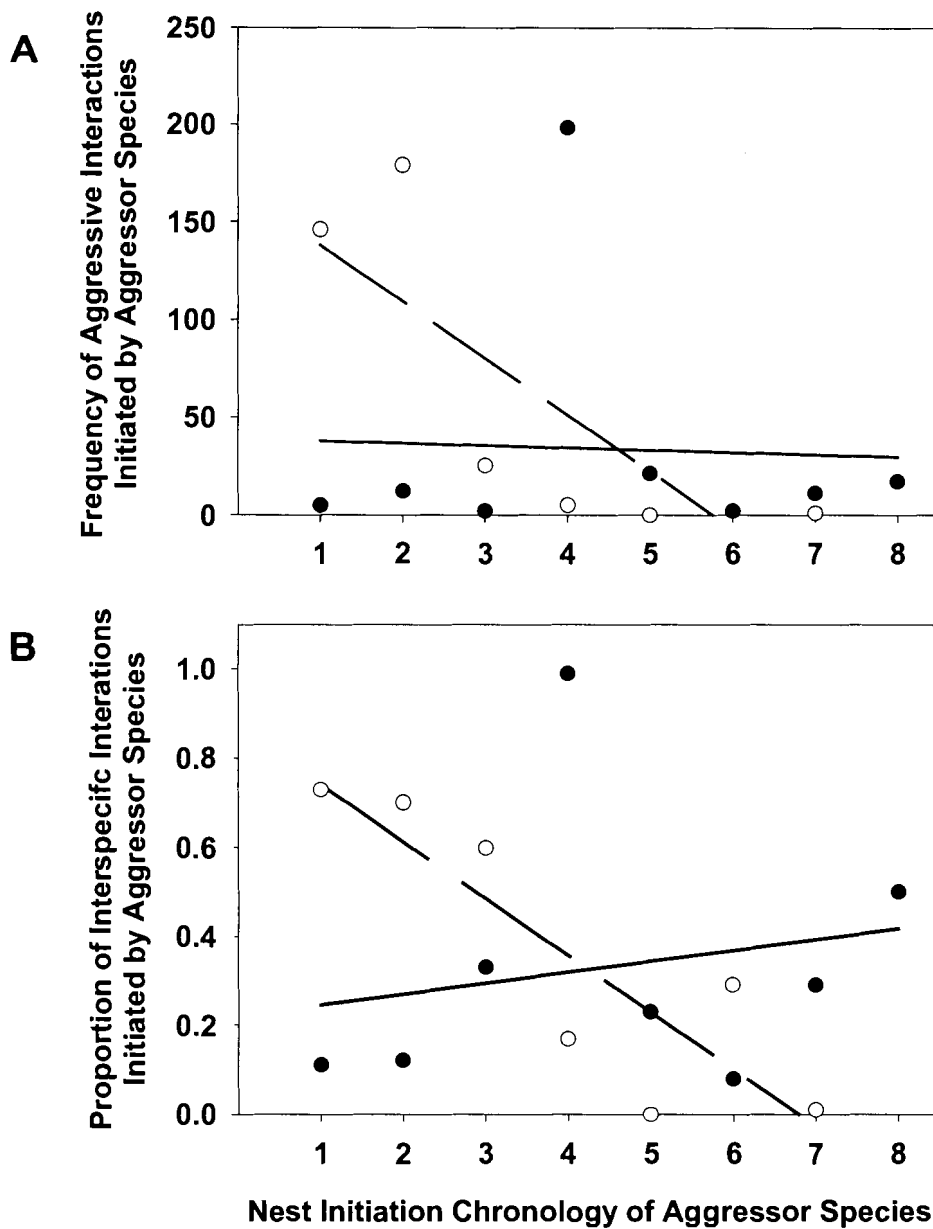


Figure 5-7 Relationships between nest initiation chronology and aggressive interactions between species of waterfowl. (A) Early-nesting species of diving ducks (open circles, dashed line) initiated more aggressive, interspecific interactions than late-nesting species (slope=-29.1; $P=0.013$; $R^2=0.66$; one-tailed test). (B) A greater proportion of interspecific interactions were initiated by early-nesting species (slope=-0.128; $P=0.005$; $R^2 = 0.76$; one-tailed test). These relationships did not hold between dabbling ducks and American Coots (solid circles, solid line) in either (A) (slope=-1.17; $P = 0.46$; $R^2 = 0.002$) or (B) (slope=0.02; $P = 0.32$; $R^2 = 0.04$).

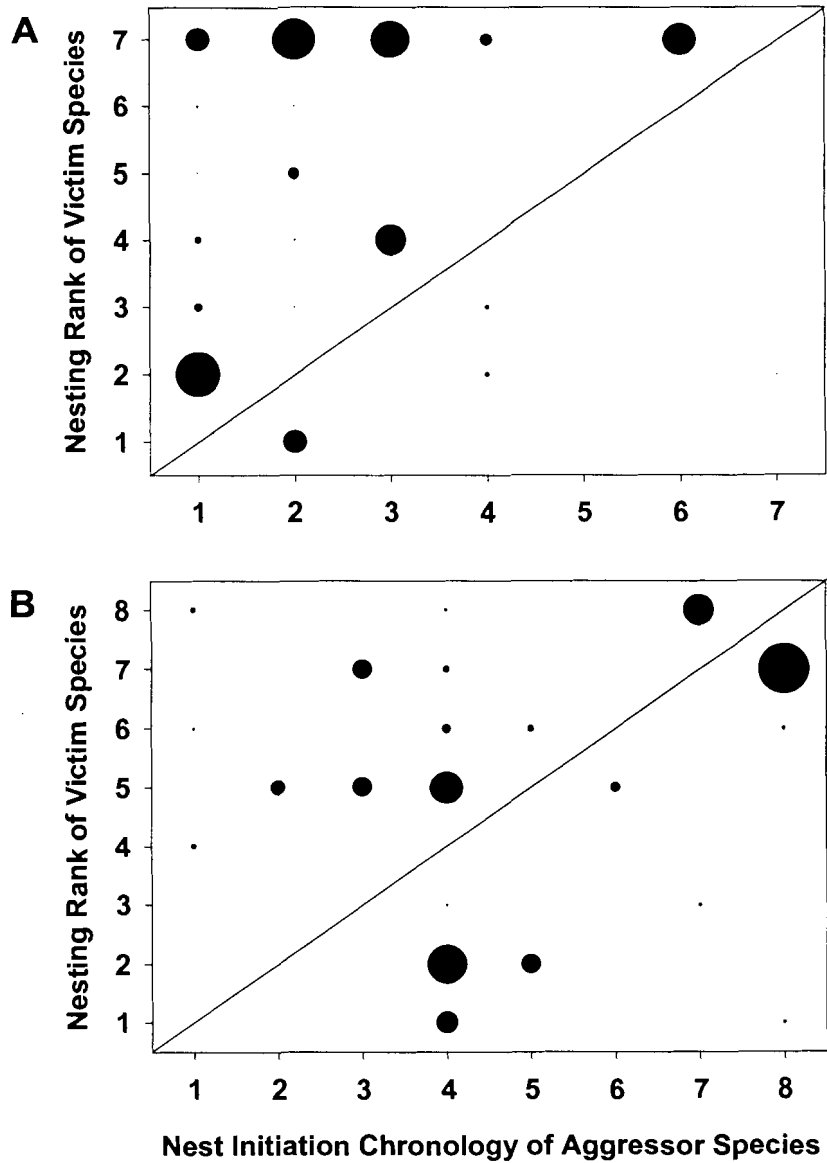


Figure 5-8 Relationships between nest initiation chronology of aggressor and victim species. The diameter of the circles indicates the proportion of interactions initiated by the aggressor species that are directed towards the victim species. (A) 84 percent of interspecific aggression initiated by diving ducks is directed towards victim species that nest after them. (B) Only 46 percent of aggressive interactions initiated by dabbling ducks and American Coots are directed towards species nesting after them. Slope of the diagonal reference lines is 1.

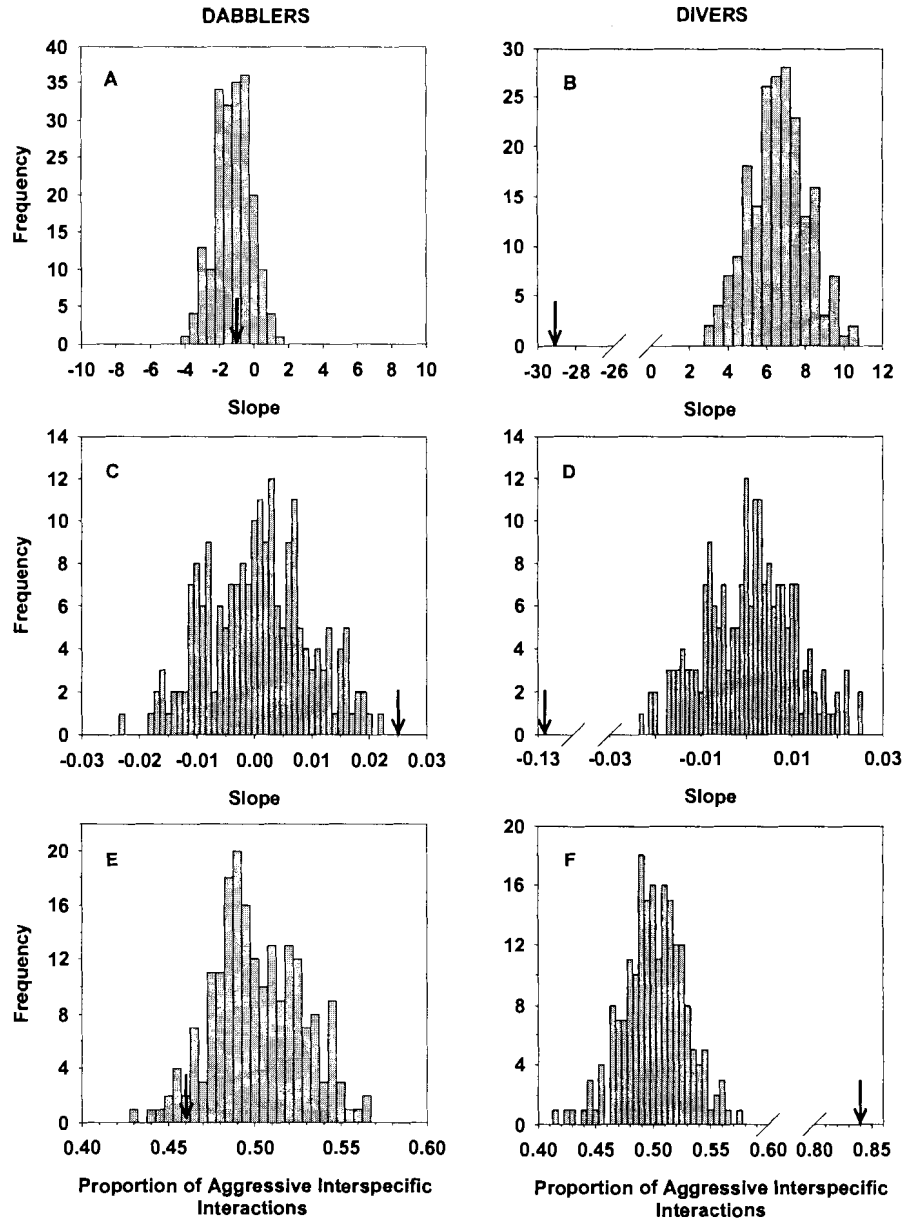


Figure 5-9 Comparison of predictions of habitat selection theory between observations (arrows) and the distribution of values expected from a null model (gray bars) for dabbling and diving ducks. The slope of the regression between frequency of aggression and nesting chronology (A, $P = 0.39$; B, $P < 0.0001$). The slope of the regression between proportion of aggressive interactions initiated and nesting chronology (C, $P = 0.014$; D, $P < 0.0001$). Proportion of aggressive, interspecific interactions initiated by aggressor species directed at victim species that nest later than the aggressor (E, $P = 0.065$; F, $P < 0.0001$).

CHAPTER 6

SUMMARY AND FUTURE PROSPECTS FOR THE STUDY OF ADAPTIVE RADIATION OF DABBLING DUCKS

6.1 Introduction

The preceding chapters have provided additional evidence and insight into the ecology of dabbling ducks. Taken together, the evidence supports the role of adaptation in the radiation in dabbling ducks. This chapter briefly summarizes this evidence in the context of the three central processes leading to adaptive radiation and suggests directions for future studies to build on the results of this thesis.

6.2 Divergent Selection Between Environments

The objective of Chapters 2, 3, and 4 were to test for a functional trade-off that linked morphology and resource type with foraging performance. Identifying such a trade-off is the first step towards testing for divergent selection using a predictive approach. Tests of the models of bill biomechanics of Mallards and Shovelers provide strong evidence that dabbling ducks face a trade-off between prey size selection and filtration rate mediated by variation in bill morphology. Future studies should test these models further by conducting foraging experiments on additional combination of prey and detritus size-frequency distributions. In particular, experiments should test combinations of size-frequency distributions that are predicted to allow Mallards to achieve greater foraging rates than Shovelers. Similar experiments should be conducted also with the other five species for which foraging models have been developed. The predictions of these models are entirely untested.

Analysis of the five years of field data I collected (including a manipulative field experiment), but did not appear in this thesis, may allow the foraging models to be tested. Analyses indicate the size-frequency distribution of invertebrates and duck use of the study ponds responded to the manipulation, but I have not compared the observed duck response to the change in foraging performance predicted by the models. Strong evidence that bill morphology

influences decisions of ducks foraging in the field will be gained if observations and predictions match.

Although this thesis has linked morphology and resource type with foraging performance, it has not tested whether selection is divergent between environments, which requires evidence of selection against intermediate phenotypes in the environments available to them. Such evidence can come from observational studies in the field that measure selection over many generations (e.g., Grant and Grant 2002), experiments conducted in the field or lab that force two phenotypes to compete with an intermediate phenotype (e.g., Schluter 1994), or demonstration that populations occupy peaks on an adaptive landscape that are separated by valleys of low fitness (e.g., Schluter and Grant 1984). Given the difficulty of working with dabbling ducks, and the predictive ability of the biomechanical models, the latter test is most feasible.

Current predictions of foraging performance from bill morphology use time-consuming simulations based on many morphological measurements (Chapter 3). Future work should replace these simulations with more powerful analytical models. Bill biomechanics are constrained by movement of skeletal elements forming a four-bar system. Algorithms defining the movement of these systems are widely available and have been used to study the trophic apparatus of fish (Alfaro et al. 2004; Hulsey and Wainwright 2002; Muller 1996). These algorithms could be used to streamline the modelling and prediction process, allowing foraging performance along a prey size gradient for a range of bill phenotypes defined by six or fewer morphological traits.

These models could then be used to estimate the foraging performance of any phenotype and, consequently, the shape of the foraging performance landscape (Arnold 2003) following Schluter and Nychka (1994). Divergent selection is supported if the mean morphology of current populations are located near peaks on the performance landscape and are separated by valleys of poor performance (Schluter and Grant 1984). The test assumes that the performance landscape corresponds well with the adaptive landscape (Fear and Price 1998).

Estimating the performance landscape requires knowledge of the size-frequency distribution of prey and detritus and is therefore environment specific. Given: (i) the correspondence between the size of seeds consumed by ducks over the winter and the size range of particles dabbling ducks can partition, (ii) the likelihood that seed availability declines over the winter and (iii) the fact most seeds will be found in benthic habitats mixed with detritus, performance landscapes should be constructed for wintering dabbling ducks that primarily consume seeds obtained from pond benthos. Data on the size-frequency distribution of seeds

available to ducks wintering in the Central Valley of California are available from J. Eadie, U.C. Davis. Mean phenotypes of existing populations can be estimated from harvested ducks and/or museum collections.

6.3 Divergent Selection Due to Negative Interactions

Chapter 5 provided correlational evidence that phenotypic divergence is caused by competition for resources. While this evidence is suggestive, additional evidence is required.

Character divergence is supported if the performance landscape predicts species mean phenotypes better when competition is included compared to the prediction when the size-frequency distribution of available seeds is considered alone (e.g., Case 1979; Schluter and Grant 1984). Because the foraging models predict the size-frequency distribution of consumed seeds, competition due to diet overlap can be included as an intrinsic component of the performance landscape. Dabbling ducks are expected to experience exploitative competition because seed abundance declines over the winter (J. Eadie pers. comm.).

Future work could use an approach similar to that of Guillemain et al. (2002). Documented declines in seed availability could be used to predict changes in the profitability of different habitat types using the foraging models and compared to foraging decisions made by ducks in the field. If the predicted profitability of habitats declines as seeds are depleted, and ducks track this change, then the role of competition is supported. Additional experiments could manipulate the size-frequency of seeds or limit species access to habitats to test more specific predictions about how predicted niche overlap affects competitive interactions between species.

6.4 Ecological Speciation

The thesis did not test for evidence of ecological speciation among dabbling ducks. Ecological speciation is the evolution of reproductive isolation in response to divergent selection acting on populations and is the last stage of adaptive radiation (Schluter 2001). Reproductive isolation can be selected directly, via reinforcement, if the fitness of hybrids with intermediate phenotypes is lower than non-hybrids, or indirectly, as a by-product of divergent selection (Schluter 2001). Consequently, the rate of hybridization is expected to decline with increasing ecological difference between species (Lu and Bernatchez 1999; McKinnon et al. 2004).

Waterfowl offer an opportunity to test this prediction because many species hybridize (Grant and Grant 1992) but at different frequencies (Tubaro and Lijtmaer 2002). However, a

method of quantifying species' ecological similarity has been lacking. The foraging models could be used to quantify niche overlap along a prey-size axis as an index of ecological similarity. If ecological differentiation has played a role in the evolution of reproductive isolation, the frequency of hybridization should decline as niche overlap declines. If reinforcement is acting, hybridization should be less frequent between species separated by deep valleys in the performance landscape. Tests of the latter prediction may be limited by the availability of data on the size-frequency distributions of resources available to some species, which are necessary to estimate performance landscapes.

6.5 Applied Paleoecology and Evolutionary Theory

The North American population of Northern Pintails (*A. acuta*) has declined since the early 1970's while populations of other species of *Anas* have not. This pattern poses two questions: what caused the decline and why did it only affect Pintails? These questions offer a unique opportunity to apply evolutionary theory to a conservation problem as well as test for evidence of resource competition and limitation in dabbling ducks. Foraging simulations indicate ducks should be able to partition the size range of naturally occurring seeds available during the winter (Chapter 4). However, the expansion of agriculture into duck wintering areas has replaced native plants with domestic crops, increasing mean seed size and reducing variation in seed size, potentially removing the variation in resources that ducks partition and increasing interspecific competition. The consequences of changing the size-frequency distribution of seeds on the foraging success of dabbling ducks could be tested using the foraging models. If the scenario above is plausible, change in the seed size-frequency distribution should cause a greater decrease in Pintail foraging performance compared to other species.

A strong test must show also that the historical size-frequency distributions of seeds provided Pintails with a niche. Wetlands and lakes are prime sampling locations for plant paleoecologists that use fossil seeds to reconstruct historical plant communities. The North American Plant Macrofossil Database provides data on the size-frequency distribution of seeds in wetlands going back thousands of years. This data, in combination with the foraging models, would allow the reconstruction of performance landscapes through an unprecedented amount of time.

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