

CHAPTER SEVEN

Foraging Behavior, Ecology, and Energetics of Sea Ducks*

Ramūnas Žydelis and Samantha E. Richman

Abstract. Sea ducks spend the majority of their life in a cold, marine environment where they must dive, often to great depths, consuming enough food to maintain energy balance. The food consumed is hard shelled, cold, and of low energetic value; yet sea ducks excel when faced with many energetic and thermoregulatory challenges, especially for a relatively small-bodied marine endotherm. The energy cost of thermoregulation and intensive work required to collect daily rations are especially high for sea ducks at high latitudes where they must cope with limited daylight for foraging under harsh winter conditions. To offset these high energetic demands, sea ducks must optimize their decisions about habitat choice, foraging behavior, and prey selection. Foraging behavior strives to maximize gross energy gain and minimize costs to reach energy balance, sometimes under the most extreme of conditions such as the polynyas of the Belcher

Islands and St. Lawrence Island. Studying sea ducks under these conditions is equally challenging but through the combined research effort of agencies, organizations, academics, and individuals, we have made great strides in gaining information on the foraging ecology of sea ducks. In this chapter, we review the general aspects of sea duck foraging ecology and diving behavior, foraging energetics, and modeling of energy balance. Each of these topics is discussed in detail, but it is not our intention to review all of the literature available, but rather to highlight the particular discoveries and developments that have greatly increased our understanding of the foraging ecology of sea ducks.

Key Words: allometry, diet composition, diving behavior, ecophysiology, energetics, foraging ecology, individual-based models, metabolic rate, thermoregulation.

Sea ducks in the Tribe Mergini are divers, capable of reaching great depths where they feed on a variety of macroinvertebrates, including molluscs, echinoderms, crustaceans, and fishes. Fish spawning events are important to the diet of sea ducks at certain times of the year but bivalves usually dominate the diet, with the exception of mergansers, which are generally

fish specialists. In this chapter, we review general aspects of sea duck foraging ecology and diving behavior, elements of energy gain and cost, and modeling of energy balance and habitat choice.

Formation of the Sea Duck Joint Venture marked the beginning of a period of coordinated investigations of sea duck ecology, which yielded significant progress in attaining new

* Žydelis, R. and S. E. Richman. 2015. Foraging behavior, ecology, and energetics of sea ducks. Pp. 241–265 in J.-P. L. Savard, D. V. Derksen, D. Esler, and J. M. Eadie (editors). *Ecology and conservation of North American sea ducks*. *Studies in Avian Biology* (no. 46), CRC Press, Boca Raton, FL.

knowledge about this group of waterbirds. With the development of remote sensing technology, we now have a better understanding of the major habitats or regions used by sea ducks throughout the annual cycle, and ground-based telemetry has provided more localized information on foraging effort, movement patterns, and habitat selection. These studies, in combination with benthic sampling, diet analysis, and data collected from captive studies, have provided information needed for models to estimate energetic carrying capacity or habitat suitability models. Individual-based models require similar types of data but attempt to answer questions at different scales from the individual to the population.

FORAGING ECOLOGY AND DIVING BEHAVIOR

Much of our understanding of animal foraging ecology is based on fundamentals of optimal foraging theory. The theory postulates that organisms forage in such a way as to maximize their net energy intake per unit time (MacArthur and Pianka 1966). The mechanistic explanation of foraging behavior and basic principles of optimal foraging theory help to explain sea duck habitat or patch selection (Kirk et al. 2008), diet choice (Beauchamp et al. 1992), and prey size selection (Bustnes 1998). However, optimal foraging theory also includes constraints such as habitat and diet specialization, digestive processing, social interactions, and anti-predator behavior (Pyke 1984), and therefore some authors dismissed this theory altogether (Pierce and Ollason 1987). Also, sea ducks may not always appear to forage optimally relative to their environment or the spatial/temporal scales of the analyses. Complexity and variability of a natural environment is usually much greater than that of experimental setups, and simple heuristic models of foraging behavior may not immediately explain bird foraging decisions observed in the wild (Heath et al. 2007). Despite debates surrounding the optimal foraging theory (reviewed by Stephens et al. 2007), we maintain that fundamentals of this theory are useful when trying to understand sea duck foraging decisions. Although this chapter does not necessarily aim to review sea duck foraging ecology in the light of optimal foraging theory, we will see that postulates of this theory repeatedly emerge.

Dive Depth and Duration

During the nonbreeding season, sea ducks typically dive for food although occasional observations suggest that in certain habitats, they can forage by head dipping or upending like dabbling ducks (Petersen 1980, Fox and Mitchell 1997, Guillemette 1998, Systad and Bustnes 2001) or even walking on reefs during low tide and eating exposed mussels (Nehls 1995). Harlequin Ducks (*Histrionicus histrionicus*), Buffleheads (*Bucephala albeola*), and Hooded Mergansers (*Lophodytes cucullatus*) typically dive to less than 5 m and use coastal habitats, while most other species aggregate in nearshore waters at depths down to 10–12 m. Long-tailed Ducks (*Clangula hyemalis*), Common Eiders (*Somateria mollissima*), and Scoters (*Melanitta* spp.) can forage over a broader depth range to 20–25 m or deeper. The deepest diving sea ducks are King Eiders (*Somateria spectabilis*) regularly foraging at 30–35 m (Bustnes and Lønne 1997, Mosbech et al. 2006) and Spectacled Eiders (*Somateria fischeri*), which use habitats 40–70 m in depth (Lovvorn et al. 2003; Figure 7.1). There are anecdotal records of Long-tailed Ducks being caught in fishing nets set at 60 m and deeper in the Great Lakes (Schorger 1947). Sea ducks can also forage pelagically without reaching the bottom, such as the Long-tailed Ducks and scoters that feed on pelagic gammarids off the coast of Southern New England near Nantucket (White et al. 2009, White 2013). Fish-eating mergansers also can forage in the water column without reaching the bottom. As a group, sea ducks utilize a rather broad range of depths, which offers them access to ample habitats within shallow seas of the Northern Hemisphere.

For most diving birds, dive time is linearly related to depths at which they are foraging: shallow diving species spend just 10–20 s underwater per dive, whereas for deeper diving species, it usually takes 30–50 s for a single dive (Figure 7.2). It was estimated that the deepest diving Spectacled Eiders in the Bering Sea, where water depths are well over 40 m, must spend about 3 min underwater in a single dive (Lovvorn et al. 2009). While diving capacity is generally linearly related to body mass in air-breathing vertebrates, no such significant relationship was found among ducks (Schreer and Kovacs 1997). It should be recognized, however, that the relationship between foraging depth and dive duration is not always simple and depends on specific habitats used at different times of the year, the type of prey consumed, and the species of sea duck.

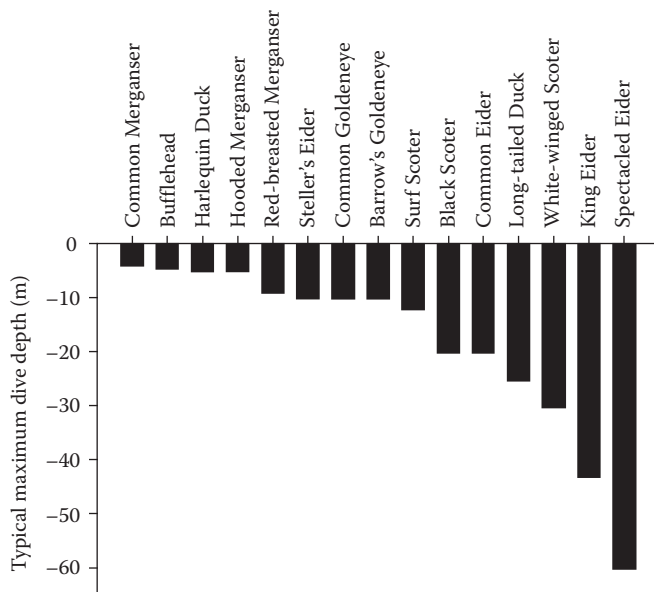


Figure 7.1. Typical maximum diving depths of sea duck species reported in the literature.

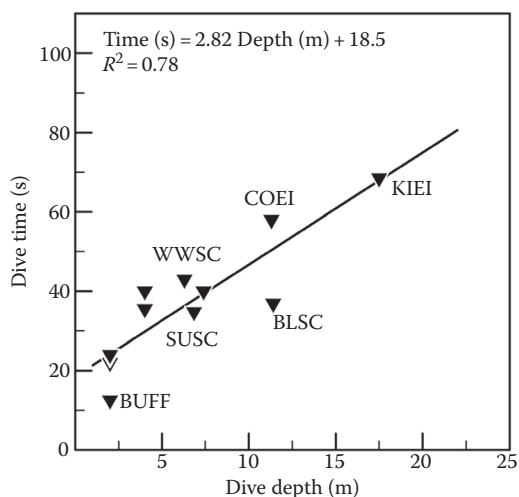


Figure 7.2. Linear relationship between diving depth and average time spent underwater by different sea duck species (time and depth values taken from Gauthier 1993, Guillemette 1998, Kaiser et al. 2006, Heath et al. 2007, Lewis et al. 2007b, Powell and Suydam 2012, Fehrnabelt Fixed Link Bird Services 2013a). BLSC, Black Scoter; BUFF, Bufflehead; COEI, Common Eider; KIEI, King Eider; LTDU, Long-tailed Duck; SUSC, Surf Scoter; and WWSC, White-winged Scoter.

Foraging Effort

Foraging behavior of sea ducks can be categorized into a dive going underwater and a short pause between consecutive dives, termed a dive cycle. Consecutive dive cycles are often followed by longer breaks (~30 min) at the surface before resuming diving; we define a series of dives separated by relatively short surface intervals as a foraging bout. During the breaks separating foraging bouts, birds usually remain at the surface or engage in other behaviors such as preening and resting. Typically, during individual dives, multiple small prey items are swallowed whole underwater, and through the foraging bout, birds fill their esophagus and proventriculus with prey. Large prey items are often brought to the surface to manipulate and handle before swallowing while the bird is replenishing oxygen stores at the same time (Lewis et al. 2008). Foraging bouts consist of 1 to >50 dives in series, depending on prey availability or accessibility and search time.

Field observations and captive studies demonstrate that sea ducks forage in bouts with multiple dives in series followed by a period of time when the food is processed and passed through the gizzard. Food processing time depends on the amount of material that has to be passed through the gizzard, which ultimately depends

on the prey species and size. No studies have specifically addressed this question of how long food is processed in the gizzard before the proventriculus is emptied allowing for another foraging bout to resume. For Common Eiders fed clams, passage rate through the digestive system (mouth to anus) was estimated to take 5 h (Richman and Lovvorn 2003), but that would include multiple foraging bouts under natural conditions. Observational studies indicate that foraging bouts and pauses between bouts are highly variable and depend on a number of biotic (prey density) and abiotic (water depth) factors, habitat, species, and prey type (Beauchamp 1992, Guillemette et al. 1992, Guillemette 1998, Goudie 1999). The amount of time that birds can spend actively foraging is important, especially when species are restricted in time available for foraging due to short day length or tidal currents. Some studies have reported that sea ducks can forage without obvious longer breaks separating foraging bouts, such as Common Eiders and Long-tailed Ducks observed in the southern Baltic Sea (Fehmarnbelt Fixed Link Bird Services 2013a). Foraging without breaks could be explained by birds' feeding on small, thin-shelled bivalves or other soft prey that can pass the gizzard quickly without a need for a digestion break (Fehmarnbelt Fixed Link Bird Services 2013a).

Most of the benthic-feeding sea ducks with large body size tend to feed for lower fractions of time during a day than small species (Figure 7.3). Despite the fact that larger species require more food in absolute terms, smaller ducks have higher mass-specific energy requirements compared to larger species (Ouellet et al. 2013). Thus, smaller species must devote more time to foraging throughout the day to maintain energy balance. Foraging activities occupy the major part of sea duck daytime activity budgets, being second only to resting (Table 7.1).

Within species, time spent foraging can vary substantially depending on many factors, both exogenous and endogenous. Foraging time of wintering Surf Scoters (*Melanitta perspicillata*) was found to increase with decreasing latitude. In Baja California, scoters spend twice as much time foraging as in Alaska and exhibit an intermediate foraging time in British Columbia (VanStratt 2011). The author suggested that such differences are determined by foraging opportunities, which apparently decline towards the southern

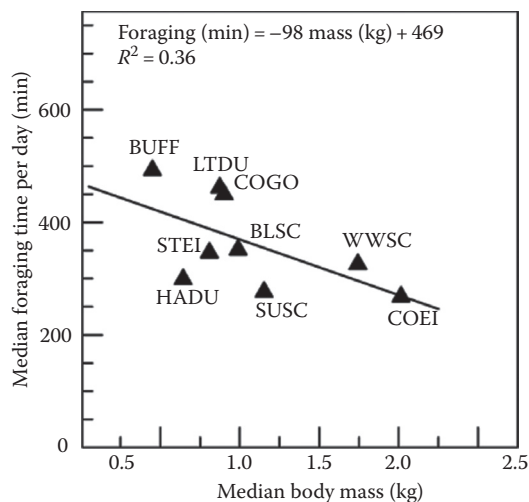


Figure 7.3. Median time spent foraging (minutes/day) during winter months, November–March, as a function of median body mass (values from Nilsson 1970, Goudie 1999, Systad and Bustnes 2001, Schummer et al. 2012, Fehmarnbelt Fixed Link Bird Services 2013a). BLSC, Black Scoter; BUFF, Bufflehead; COEI, Common Eider; COGO, Common Goldeneye; HADU, Harlequin Duck; LTDU, Long-tailed Duck; SUSC, Surf Scoter; STEI, Steller's Eider; and WWSC, White-winged Scoter.

periphery of the distribution range. Surf Scoters in Baja California had a diet of infaunal invertebrates such as ghost shrimp (*Callinassa* spp.) compared to a mostly bivalve diet further north, and in Baja worked hard to collect their daily ration (VanStratt 2011). The northern distributional limit of wintering sea ducks can be determined by daylight. Being primarily diurnal foragers, sea ducks are constrained by short day length at high latitudes, and to maintain energy intake, they increase foraging intensity (Guillemette 1998, Systad et al. 2000). Ambient temperature also has an effect; in colder environments, sea ducks tend to feed more, probably to compensate for increased thermoregulatory demands (Nilsson 1970, Goudie and Ankney 1986, Schummer et al. 2012). However, birds can also increase foraging effort when trying to accumulate fat deposits before long-distance migrations and (or) breeding, a phenomenon known as hyperphagia (Guillemette 2001, Hario and Öst 2002, Rigou and Guillemette 2010, Oppel et al. 2011).

Prey abundance and caloric value also have direct effects on foraging effort. Scoters spend less time diving for the abundant and nutritious eggs of Pacific herring (*Clupea pallasii*) than when

TABLE 7.1

Several examples of sea duck activity budgets shown as percent of daytime spent per certain activity during wintering period.

Species	Location	Month	Activity type					Sources
			Feeding	Resting	Locomotion	Comfort	Social	
Harlequin Duck	Haida Gwaii, BC	Oct–Feb	51–68	22	10	5	3	Goudie (1999)
Black Scoter	Haida Gwaii, BC	Oct–Feb	53–76	18	8	3	1	Goudie (1999)
Steller's Eider	Izembek, AK	Sep–Mar	70	5	8	15	1.7	Laubhan and Metzner (1999)
	Cold Bay, AK	Sep–Mar	80	1	14	4	1.4	Laubhan and Metzner (1999)
Surf Scoter	Haida Gwaii, BC	Oct–Feb	40–70	21	12	5	2	Goudie (1999)
White-winged Scoter	Haida Gwaii, BC	Oct–Feb	54–75	23	6	6	1	Goudie (1999)
	Puget Sound, WA	Nov–Feb	23–30	11–23	34–44	10–18		Anderson and Lovvorn (2011)

Feeding activity represents foraging bouts, that is, dive and short pauses between consecutive dives. See sources for specific details.

foraging on bivalves (Lewis et al. 2007b). Foraging time increases as prey is depleted (Kirk et al. 2007, Anderson and Lovvorn 2011, VanStratt 2011, Bustnes et al. 2013) or birds completely abandon a depleted area (Kirk et al. 2008, Lovvorn et al. 2013). However, duck responses to depleted food resources vary by habitats and prey type. For example, Surf Scoters in British Columbia were found spending similar amounts of time foraging in three habitat types differing by bivalve prey species, the nutritional content, quality, and quantity, which suggests that despite variations in prey landscapes, Surf Scoters are able to maintain similar intake rates by redistribution and habitat selection (Kirk et al. 2007). Several response mechanisms to changing prey abundance have been observed. For example, Common and King Eiders wintering in northern Norway increased their foraging effort, redistributed themselves within habitats, and dispersed into smaller flocks as food resources declined over winter (Bustnes et al. 2013). These examples imply high adaptability of sea ducks to varying environmental conditions and an ability to employ multiple foraging strategies when responding to changing prey availability or moving between habitat types.

A rather interesting phenomenon is synchronous group foraging of some sea duck species. Sea ducks are often gregarious during nonbreeding periods, rafting together in large groups. When birds are in groups, synchronous foraging occurs when the entire flock dives simultaneously, and

has been documented in Surf Scoters, Barrow's Goldeneyes (*Bucephala islandica*), Common Eiders, and Steller's Eiders (*Polysticta stelleri*, Schenkeveld and Ydenberg 1985, Beauchamp 1992, Guillemette et al. 1993, Laubhan and Metzner 1999). Benefits of synchronous foraging are not fully understood; however, synchrony might help reduce kleptoparasitism by conspecifics and gulls (Schenkeveld and Ydenberg 1985) and maintain flock cohesion during dives (Beauchamp 1992).

Nocturnal Foraging

Sea ducks are thought to be visual foragers and to limit their foraging activity to daylight hours (Owen 1990, McNeil et al. 1992). However, to cope with reduced daylight at high latitudes, some species may feed well after sunset (Systad et al. 2000, Systad and Bustnes 2001). Radio telemetry revealed that Surf Scoters and White-winged Scoters (*Melanitta fusca*) essentially do not dive at night in Baynes Sound, British Columbia (Lewis et al. 2005). Similar results were reported for Harlequin Ducks in Prince William Sound, Alaska (Rizzolo et al. 2005), and for Common Eiders and Long-tailed Ducks in the southern Baltic Sea (Fehmarnbelt Fixed Link Bird Service 2013a). No nocturnal foraging was observed among Common Eiders wintering in the Gulf of St. Lawrence (Guillemette 1998) or in the polynya near the Belcher Islands of Hudson Bay (Heath and Gilchrist 2010). However, under certain

conditions or in particular habitats, nocturnal foraging of sea ducks has been observed for several species. Systad and Bustnes (2001) reported nocturnal foraging of Steller's Eiders in northern Norway (70°N) in midwinter and explained this behavior as an adaptation to the short period of daylight and the cold environment. It is also known that molting Common Eiders regularly forage at night in tidal habitats of the Wadden Sea (Nehls 1995) and nocturnal diving was recorded during 10% of the time Common Eiders spent foraging in Denmark (Pelletier et al. 2007). Common Eiders wintering in southwest Greenland use two foraging strategies. They are diurnal foragers in an outer coastal habitat and primarily feed at night in a fjord habitat; the latter strategy was explained as predator avoidance behavior (Merkel and Mosbech 2008). Surf Scoters also forage during day and night in the southern periphery of their wintering habitat of Baja California (VanStratt 2011). In summary, at least some species of sea ducks are capable of feeding in the dark, although diurnal foraging clearly prevails.

Diet Composition

Among the sea ducks, Red-breasted Mergansers (*Mergus serrator*) and Common Mergansers (*M. merganser*) are obligatory piscivores that forage on small (10–15 cm long) and medium-sized fish (10–30 cm), respectively. Prey composition varies with water body and geographic location and typically represents the most abundant fish species of suitable size (Mallory and Metz 1999, Titman 1999). Hooded Mergansers have a more diverse diet where fish comprise about one half of their food, while aquatic insects, crustaceans, crayfish, and molluscs are eaten regularly (Dugger et al. 2009). Anderson et al. (2008) reviewed the diets of sea ducks that forage on diverse taxa, with small sea ducks typically consuming a mix of bivalves, gastropods, crustaceans, and fish, while diets of scoters and eiders consist of mostly bivalves and, to a lesser extent, crustaceans and echinoderms. Some species, such as White-winged Scoter and Spectacled Eider, specialize in foraging on clams and other infaunal prey, while goldeneyes, Harlequin Ducks, and Common Eiders are epifaunal specialists and feed predominately on prey living on the surface of bottom substrate or on submerged vegetation. Long-tailed Duck, Surf Scoter, and Black Scoter (*Mergus americana*) are considered generalist

foragers because they readily feed on either infauna or epifauna, depending on habitat. While these generalizations reflect predominant food choices of sea ducks, there are exceptions. For example, chitons were the major food item of Common Eiders in Iceland (Kristjánsson et al. 2013), sea urchins and crabs comprise a substantial proportion of Common Eider diet in the Gulf of St. Lawrence (Guillemette et al. 1992), and fish are eaten by Common Eiders in the Netherlands (Leopold et al. 2012). Sea duck diets were summarized and conceptualized by Ouellet et al. (2013) who suggested that smaller species use a risk-prone foraging strategy and search for higher-quality, less-abundant prey in part because of their higher mass-specific metabolic rate. In contrast, larger species typically feed using a risk-averse strategy to maximize intake of lower quality but predictably abundant prey. Due to body mass and time constraints, diurnally feeding, small-sized sea ducks would not be able to achieve positive or neutral energy balance if they foraged on voluminous prey of low caloric value, as size of a single meal and a number of meals per day is limited by the birds' morphology and day length (Ouellet et al. 2013). This hypothesis is further supported by activity budgets of sea ducks; the proportion of time spent foraging is inversely related to species size (Figure 7.3).

Sea ducks readily switch their diets to ephemeral but abundant foods. Many species, including Harlequin Duck, Long-tailed Duck, White-winged Scoter, Surf Scoter, and Steller's Eider, turn to feeding on fish eggs when available during mass spawning events. Such phenomena have been documented in British Columbia and Alaska (Rodway 2003, Lewis et al. 2007a, Anderson et al. 2009, Lok et al. 2012), northern Norway (Bustnes and Systad 2001), and the Baltic Sea (Stempniewicz 1995, Žydelis and Esler 2005). Large aggregations of Surf Scoters, along with a few other duck species, have also been recorded at a site where mass spawning of marine polychaetes took place (Lacroix et al. 2005). Another type of opportunistic foraging behavior has been observed in Puget Sound where Surf Scoters and White-winged Scoters were diving next to feeding gray whale (*Eschrichtius robustus*), which presumably exposed benthic invertebrates by disturbing large amounts of bottom sediments (Anderson and Lovvorn 2008). Similarly, Long-tailed Ducks were regularly observed diving in the wake of the Nantucket Island ferry where

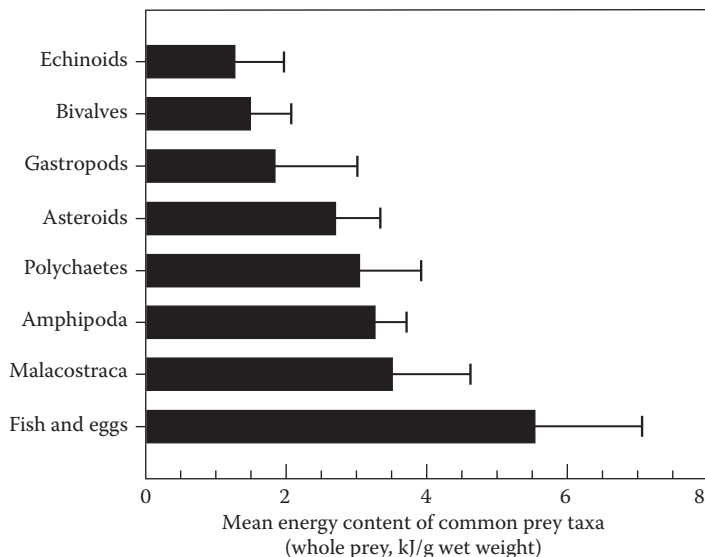


Figure 7.4. Average energetic values (\pm SD) of principal sea duck prey expressed as kilojoules per gram of fresh mass of the whole organism. Prey energetic values adapted from Ouellet et al. (2013) and Rumohr et al. (1987).

they presumably forage on prey dislodged by the ship propeller (Perry 2012).

Most sea duck foods are of low caloric density with high inorganic content such as sea urchins, molluscs, and crustaceans, while polychaetes, fish, and fish eggs are of high energy density and easily digestible (Figure 7.4). However, energetic value of prey varies substantially by size, season, and stage of reproductive cycle. For example, variation in energy contents of filter-feeding bivalves may range up to 100% throughout the year depending on reproductive stage, phytoplankton availability, and ambient temperature (Bayne and Worrall 1980, Kautsky 1982, Waldeck and Larsson 2013). The flesh-to-shell ratio depends on bivalve size and habitat (Bustnes and Erikstad 1990, Bustnes 1998, Kirk et al. 2007). Therefore, variation in prey energy between locations should be considered whenever possible to most accurately assess the energy intake of sea ducks.

Methods for Studying Sea Duck Diets

Analysis of esophagus and gizzard contents of dead birds is an important method to examine prey species, size preference, and overall diet composition of sea ducks. However, gut content analysis has limitations as (1) soft-bodied prey are often underrepresented because of rapid digestion in the foregut, (2) the esophagus and gizzard

typically contain food from only a single meal and may not be representative of an individual bird's diet, and (3) the sample size is usually limited.

Some information about sea duck diet composition could be collected using focal observations of foraging birds and recording food items brought to the water surface (Lewis et al. 2008), or analyzing remnants of hard prey in bird droppings (Lewis et al. 2007b). These methods can be representative of diets dominated by large bivalve prey, which sea ducks usually handle at the surface (Ydenberg 1988, de Leeuw and van Eerden 1992). However, small or soft-bodied prey would be missed in analyses despite often comprising an important proportion of the diet (Richman and Lovvorn 2004, Anderson et al. 2008).

The challenge in comparing diet studies of species that are often located far from shore is to collect ducks under similar or consistent protocols (Anderson et al. 2008). Authors reporting results of direct diet examination use a range of metrics, including prey counts, frequency of occurrence, percent wet mass, dry mass, ash-free dry mass, and volume, with little consistency, but chosen metrics have important consequences to interpretation. When possible, diet composition should be reported in several standard metrics such as percent composition of prey by mass and percent frequency of occurrence, as well as an index of the size of prey. Multiple metrics are especially

important when only biomass (g) is reported. For example, diet items such as clams or mussels can span a large range in sizes that are consumed by ducks; however, shell mass increases exponentially with increasing length, but to a lesser extent for meat content. Thus, a single, individual mussel >80 mm in length can have similar biomass as 30 smaller clams, but because the smaller clams can be easily ingested while underwater, only the smaller clams will be consumed. Also, the total or mass-specific energy content of mussels increases with increasing length to an optimum, before energy content relative to shell fraction declines. For many of the large sea ducks like Common Eider and White-winged Scoter, we unexpectedly find dietary preferences for smaller prey items than we would expect for their body size. Video observations have shown eiders consistently digging between larger prey clumps or near the surface of the sediment in search of smaller mussels (S. E. Richman, pers. obs.). Thus, it is important to report the size composition of ingested prey because energy content can vary with prey size.

Estimating Diet with Biochemical Markers

An alternative to direct diet analysis is the application of stable isotope and fatty acid analyses to describe animal diets and trace migratory origins. Stable isotopes of carbon, hydrogen, oxygen, and even sulfur have revolutionized the way we view animal diets. When differences exist between diets or habitats, biochemical markers can determine how nutrients are allocated from resources to blood, feathers, claws, eggs, and other tissues. For example, a recent major development in the way we understand contributions of endogenous nutrients from the body versus exogenous nutrients from the diet to egg formation by laying female birds involves diets that differ in source nutrients (reviewed by Hobson 2006; Schmutz et al. 2006; Bond et al. 2007; Chapter 5, this volume). This approach has been largely successful in quantifying nutrient allocations but relies on an untested assumption that the isotopic link between endogenous body tissues to eggs laid under a strictly capital strategy resembles that of a carnivorous bird under a purely income strategy (Gauthier et al. 2003). The true capital discrimination factor remains elusive because it is generally difficult to get birds to lay in captivity without food.

To obtain more definitive results from this promising method, we first need to develop species-specific calibration coefficients and discrimination factors on known, homogenized diets. Combination of fatty acid analysis and compound-specific stable isotope analysis (CSIA) would allow quantifying consumer diets and tracing animal diet sources. Using fatty acids from consumers and a comprehensive diet library combined with calibration coefficients that account for consumer metabolism, it is possible to estimate the proportion of diet items in the consumer (quantitative fatty acid signature analysis; Iverson et al. 2004, Wang et al. 2010). Similarly, CSIA focuses on tracking the isotopic signature of specific fatty acids that can only arise from diet. Thus, these dietary fatty acids in an animal should reflect that of the diet source (Budge et al. 2008, 2011). Although these methods have been developed for some of the marine food webs, we could begin acquiring common prey items for sea ducks to contribute to a fatty acid library. At that time, we may be able to apply these methods to the field.

FORAGING ENERGETICS

An approach to foraging energetics is to determine the components of an animal's energy budget that are considered important, such as activity in flight, diving, or resting, and then test those values to see if they are sensitive to a change. Energetic modeling can be approached in a number of ways, but all methods have the same underlying theme of trying to determine gross energy in minus energy costs. The amount of effort an animal must expend to acquire enough resources to maintain a positive energy balance can be broken down into measurable components. Energetics can be viewed as a conceptual flow chart analogous to a cost-benefit relationship in economics, where an animal must balance energy cost with energy gain, and is the basis for our approach for energy balance (Figure 7.5, adapted from Lovvorn et al. 2009).

For a sea duck foraging in a given habitat, prey is often distributed in dense patches that must be found during the search time. For our purposes, we assume that a bird has found a prey patch and the amount of food that is consumed by a duck during a dive is determined by the prey type (taxa), density of prey, and the size structure of prey. To maintain energy balance, an individual will expend energy to find, consume, and process food,

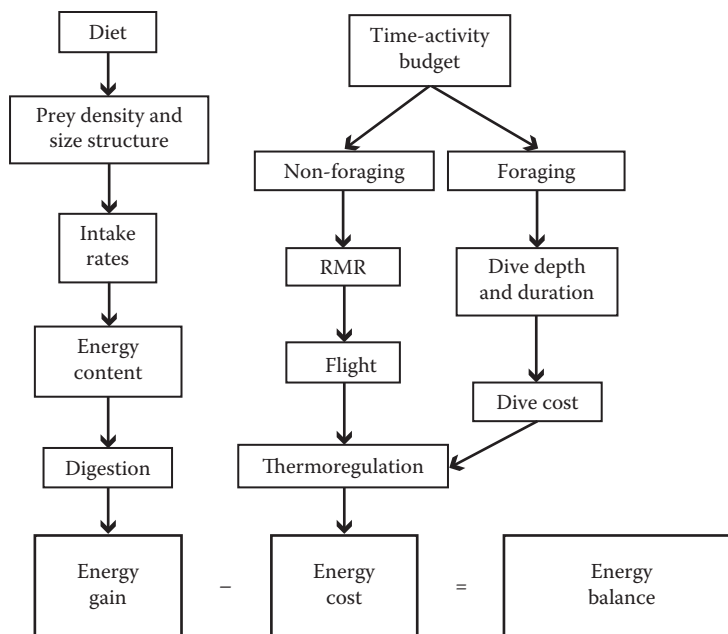


Figure 7.5. Flow chart of the energy balance approach. (Adapted from Lovvorn et al. 2009.)

in addition to maintenance metabolism, different activities such as diving, flying, or swimming, growth, and production of waste products. Here, we will use this energetic approach to evaluate the elements of energy gain and cost for sea ducks. Elements of energy gain incorporate the availability and accessibility of prey and the rate of ingestion and digestion. Elements of energy cost, on the other hand, include the amount of time an animal spends in a particular activity multiplied by the cost of that activity and additional costs of thermoregulation. Here, we briefly discuss individual components on energy gain and cost and describe how these factors allow sea ducks to be successful in the marine environment. Studies of captive birds and field experiments have improved our understanding of how sea ducks allocate energy for daily or seasonal activities, which will influence when and where they migrate or reproduce, as well as habitat selection and ultimately survival.

ELEMENTS OF ENERGY GAIN

The amount of energy gained by a predator varies widely between different prey types such as mussels versus herring spawn and often changes considerably by prey size, season, and location. The blue mussel (*Mytilus edulis*) is a common bivalve prey for

many sea ducks but tends to be smaller and thinner shelled at aquaculture sites than populations of the same species in intertidal areas (Kirk et al. 2007) and has a different shell size and composition when growing in warmer and often brackish waters of the Baltic (Kautsky et al. 1990). These different characteristics of primary prey such as mussels or clams, as well as overall species composition, abundance, and size structure of benthic prey communities, all have important consequences to the amount of food consumed (Zwarts and Wanink 1993; Richman and Lovvorn 2003, 2009; Merkel et al. 2007; Lovvorn et al. 2009). Thus, gross energy gain depends on all of these factors and especially the availability and accessibility of prey within a habitat.

For clarity, our discussions of energy budgets will use calories (cal), joules (J), and watts (W) as principal units because they are easily inter-converted (1 cal = 4.184 J or 1 J = 0.2389 cal, 1 W = 1 J/s). Note that W and W/kg are not the same measures and the mass of the animal should always be reported so that energy costs can be compared among species and studies.

Energy Intake

Gross energy intake was presented by Richman and Lovvorn (2008) in a comparison of foraging

profitability (energy intake minus cost) and threshold prey densities (the density at which energy balance becomes positive), for captive scaup (*Aythya* spp.) and White-winged Scoters foraging in a dive tank using the following equation:

$$\begin{aligned} \text{Energy intake (J/dive)} \\ = \text{Intake}_{\text{size,depth}} \times \text{AE}_N \times \text{Energy} \times \text{Time}_{\text{bottom}} \end{aligned}$$

where energy intake is calculated for individual dives (J/dive). It is important to recognize the unit of choice when estimating energy intake where intake rates are based on functional response curves generated for White-winged Scoters feeding on clams (18–24 and 24–30 mm in length) at a burial depth of 4 or 6 cm in sand (Richman and Lovvorn 2003, 2008). Diving ducks typically show a type II functional response where intake rates are an increasing function with increasing prey density (number of individual prey items/m²) up to a maximum when a bird can only eat so many per second (Richman and Lovvorn 2003). Intake rates are the number of prey items consumed per second while the bird is at the bottom. Energy intake for a particular prey item is then adjusted for the proportional assimilation efficiency (AE_N), which is the amount of ingested energy absorbed by the gut corrected for nitrogen retention (~70% for eiders fed clams, Richman and Lovvorn 2003). For White-winged Scoters in a large dive tank, intake rates for prey of differing size and depth in the substrate influenced the amount of energy gained while foraging at the bottom with larger prey and deeper burial depths resulting in lower intake rates (Richman and Lovvorn 2003, 2004). Perhaps the handling associated with larger prey as well as the extra time needed to excavate larger clams from sediments explains the reduced intake rates.

For maintaining positive energy intake, the sum of foraging time and digestive processing may not exceed the total time available for foraging. Because sea ducks consume prey whole, preference for smaller bivalves than expected has been explained by differential availability, handling times, effects of meat/shell ratio on nutrient gain relative to passage rates, or as a means of avoiding prey that are too large to be swallowed (Bustnes and Erikstad 1990). Resistance of shells to crushing in the gizzard may also affect selection of species and sizes of bivalve prey (Navarro et al. 1989). Further, shell lengths that are most

often consumed by sea ducks are 10–30 mm, which may be optimal in terms of the ratio of proportion of meat to the cost of crushing the shell (Bustnes and Erikstad 1990, Nehls 1995, Hamilton et al. 1999).

The time required to process food in the gut can be longer than the time needed to find, handle, and ingest food (Jeschke et al. 2002). Further, passage times through the gut vary widely among prey types. Soft-bodied prey may travel more quickly through the digestive system than mussels that must be crushed in the gizzard before moving into the small intestine. Differences among prey in retention time in the gut can therefore affect acquisition of nutrients and energy (Guillemette 1994, 1998). To complicate matters further, waterfowl show great phenotypic flexibility and rapid adjustments in gut morphology, altering gut capacity, volume, rates of uptake, and absorption (Goudie and Ankney 1986, McWilliams and Karasov 2001).

Body Reserves

If energy intake exceeds energy demands, birds can store energy as body reserves for use during periods when energy expenditure exceeds nutritional intake. Of four basic body components, protein, lipid, mineral, and water, lipid is the main energy reserve because it has minimal structural functions and can be catabolized (Schamber et al. 2009). The energy content of lipid at 39.3 kJ/g is more than twice that of protein at 17.8 kJ/g (Schmidt-Nielsen 1975). Birds use lipid reserves as a buffer in uncertain foraging and environmental conditions, as an energy source to fuel long-distance migrations, and as extra energy for egg production and fasting during the nesting period.

Lipid reserves are an excellent source of energy for birds that must dive and fly. Both lipid and protein yield a lot of energy; however, proteinaceous tissue is more than 70% water and therefore heavier than lipids. The low water content of lipid makes it an ideal storage form although it is a common misconception that having higher lipid reserves for diving birds will influence dive costs due to increase costs of buoyancy. While lipid and adipose tissues are far more buoyant than proteinaceous tissue like muscle, subcutaneous fat provides insulation that does not compress with depth underwater unlike the air layer in the plumage, which is the

primary source of insulation for sea ducks. Since the buoyancy of air is nine times greater than that of lipid, air spaces in the respiratory system and plumage are far more influential to diving birds. Birds can make small adjustments of air spaces and easily compensate for any buoyancy changes due to changes in lipid stores (J. R. Lovvorn, Southern Illinois University, pers. comm.).

Body reserves of shorebirds on average consisted of 85% lipid, 10% water, and 5% protein (Kersten and Piersma 1987), and similar levels might be expected for sea ducks. These authors also reported that for 1 g increase in body mass, a bird needs 45.7 kJ of additional energy intake at the energy deposition efficiency of 88%. Body mass is often used to assess bird body condition, especially when mass is used together with additional body size metrics (Schamber et al. 2009). Dynamics of sea duck body condition throughout the annual cycle reflect strategies of nutrient balance and reveal potentially critical periods for birds. Body mass in waterfowl typically is low following the breeding season and through molt but increases in the autumn, declines throughout the winter, and increases again prior to spring migration (Hepp et al. 1986, Kestenholz 1994). Sea ducks follow a similar trend in body mass dynamics (Pettersson and Ellarson 1979, Anderson and Lovvorn 2011, Schummer et al. 2012, Palm et al. 2013). Maintaining high body mass in early winter could be viewed as an adaptation when the uncertainty of sufficient food intake during the shortest days of the year and possible harsh winter weather conditions may pose constraints on energy intake. The uncertainty of limited food resources or foraging time presumably relaxes as days get longer with progressing winter and subsequently birds do not need to invest in carrying extra reserves. However, body mass could also decline as a result of not meeting daily nutritional demands due to depletion of food (Anderson and Lovvorn 2011) or severe environmental conditions (Schummer et al. 2012). Wintering White-winged Scoters were found to maintain highest body mass at an exposed offshore site where birds faced unpredictable food resources and increased thermoregulatory costs compared to sheltered nearshore sites in British Columbia and Washington State (Palm et al. 2013). Interestingly, this study showed that despite varying scoter body mass at different sites, levels of plasma metabolites varied little indicating that White-winged

Scoters at all sites maintained physiological homeostasis (Palm et al. 2013).

ELEMENTS OF ENERGY COST

Sea ducks face many challenges to living in a marine environment where maintaining body temperature in cold water is energetically expensive. Nevertheless, Long-tailed Ducks, Steller's Eiders, and goldeneyes are small-bodied sea ducks that inhabit cold water in polar and subpolar regions alongside large-bodied ducks like Common Eiders and Scoters. In these habitats, energy expenditure is high for maintenance metabolism, foraging and nonforaging activities (including flight and diving), and thermoregulation.

Maintenance Energy Costs

Basal metabolic rate (BMR) is the measure of the lowest rate of energy expenditure for individuals that are sexually and physically mature, postabsorptive, at rest, and within a thermoneutral environment (Kleiber 1932). We often use BMR as a common benchmark for comparing species using allometric relationships with body mass on a log scale. However, sea ducks rarely satisfy the conditions for basal metabolism and are always well above those predicted from standard allometric equations (Ellis and Gabrielsen 2002). A more practical measure of metabolism for sea ducks, which includes thermoregulatory costs, is resting metabolic rate (RMR). We can then measure activity-specific metabolic rates such as the costs of swimming, preening, or diving. Daily energy expenditure (DEE) is estimated as the duration of different activities multiplied by their respective costs and summed for 24 h per day. While we often focus on activities of high apparent cost like diving or flying, these activities may occupy a relatively small fraction of the day (Table 7.1). While at sea, sea ducks can spend 40%–80% of their day floating on the water surface, making resting costs the largest component of their DEE. Using a spatially explicit simulation model, Lovvorn et al. (2009) showed that for Spectacled Eiders in the Bering Sea, diving and flying were a minor part of the overall energy budget.

Metabolic rates for a few species of sea ducks have been measured in both air and for birds floating on water at varying temperatures. While differences in experimental setup and behavior

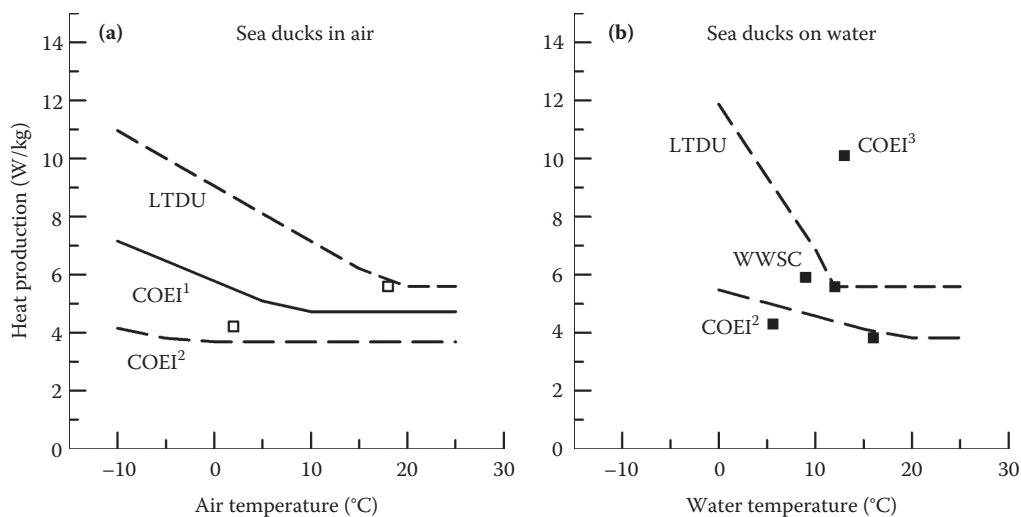


Figure 7.6. RMR for sea ducks in air (a) and floating on water (b) at varying temperatures. Regression lines for single studies in which data were collected over a range of temperatures are given in Table 7.2 (Richman and Lovvorn 2011). COEI, Common Eider (¹Gabrielsen et al. 1991, ²Jenssen et al. 1989, ³Hawkins et al. 2000), WWSC, White-winged Scoter, and LTDU, Long-tailed Duck.

state of the birds make comparisons a challenge, Richman and Lovvorn (2011) found that sea ducks were far more resistant to heat loss than other species of sea birds (Figure 7.6, Table 7.2). In fact, for Common Eiders, there was little difference in RMR between air and water at any temperature. For much smaller Long-tailed Ducks, metabolic rates in air and water were similar above 10°C but increased faster in water at lower temperatures and rose more rapidly than for other larger species of sea ducks (Richman and Lovvorn 2011). Common Eiders showed no clear lower critical temperature in air or on water (Jenssen et al. 1989), perhaps because of their large body size and thick plumage air layer.

A major challenge, however, is the variation and inconsistencies in measures of metabolic rates that may have important implications for energetics models. For example, the metabolic rate of Common Eiders while floating on water at 16°C was measured as 3.83 W/kg by Jenssen et al. (1989), but 10.1 W/kg at similar temperatures (14°C–19°C) by Hawkins et al. (2000). If we were to construct a time–energy budget for a Common Eider floating on water at 15°C for a conservative estimate of 17 h a day (Systad et al. 2000), the total daily cost of resting on the water surface would be ~457 kJ if we used 3.83 W/kg versus 1,100 kJ/day if we used 10.1 W/kg. The differences in the estimates would

more than double the amount of food required per day, an anomaly that would increase if the trend were extrapolated to lower water temperatures (Richman and Lovvorn 2011). For sea ducks that spend far more time resting on water than actively diving, valid estimates of RMR are critical to models of energy balance used to estimate of the amount and quality of habitat they need (Lovvorn et al. 2009).

Activity Costs

Cost of Flight

Nonbreeding sea ducks spend small portions of their day engaged in social activities, preening, or flying, except for migration periods. Using implantable data loggers, Pelletier et al. (2007, 2008) found that nonmigrating Common Eiders fly on average only about 10 min/day. No similar information is available for other sea duck species, but they probably do not spend more than 1%–2% of their time in flight. Although the proportion of time spent flying for sea ducks may be low, the relatively high energy cost of flight means that it cannot be ignored when estimating energy expenditures.

The energy costs of flying can be estimated using freely available software (Program Flight, Pennycuik 2008). The only input parameters

TABLE 7.2
Resting metabolic rate in air (RMR_{air}) and on water (RMR_{water}) and mean body mass.

Species	N	Mass (kg)	RMR (W)	T_{obs} ($^{\circ}C$)	T_{lc} ($^{\circ}C$)	Regression (Below T_{lc})	RQ	Sources
In Air								
Common Eider	12	1.66 ± 0.25	4.75 ± 0.39	>7	7	$5.81T_A - 0.14T_A$	0.70	Gabrielsen et al. (1991)
	6	1.79 ± 0.13	4.22 ± 0.35	>2	2		0.77	Hawkins et al. (2000)
	7	1.66 ± 0.17	3.68 ± 0.48	>1.5	1.5	$3.46T_A - 0.07T_A$	0.71	Jenssen et al. (1989)
Long-tailed Duck	5	0.49 ± 0.03	5.6 ± 0.32	>18	18	$9.06T_A - 1.9T_A$	0.71	Jenssen and Ekker (1989)
On Water								
Common Eider	7	1.79 ± 0.13	10.10 ± 2.027	13.7–19			0.77	Hawkins et al. (2000)
	10	1.80 ± 0.09	4.3 ± 0.3	5.6			0.85	Jenssen and Ekker (1991)
	5	1.95 ± 0.09	3.83 ± 0.24	16–25	16	$5.48T_w - 0.09T_w$	0.71	Jenssen et al. (1989)
White-winged Scoter	5	1.09	5.91	9			0.80	Richman and Lovvorn (2008)
Long-tailed Duck	5	0.49 ± 0.03	5.59 ± 0.56	>12		$11.87T_w - 0.50T_w$	0.70	Jenssen et al. (1989)

Measures of resting metabolic rate (RMR), the observed temperature (T_{obs}) in air (T_A) or while floating on water (T_w), and lower critical temperature (T_{lc}). In each study, the respiratory quotient (RQ) was calculated directly from the ration of CO_2 production to oxygen consumption (from Richman and Lovvorn 2011).

required for this mechanical flight model are body mass, wing span, and wing area, and for many bird species, these morphometric measures are available in Alerstam et al. (2007). Sea ducks have a relatively small wing area and consequently high wing loading (body mass divided by wing area), and as a result, they are fast fliers (Lovvorn and Jones 1994, Alerstam et al. 2007). Fast flight, however, is energetically expensive, ranging from 67 to 99 W/kg for the assessed species (Figure 7.7). Flight costs do not correlate with bird mass, but it seems that mergansers, which pursue their prey underwater, have the lowest flight costs compared to ducks that forage on sessile benthic prey. Lovvorn and Jones (1994) tested the hypothesis that high wing loading in foot-propelled divers could be an adaptation to diving; however, they concluded that wing morphology is probably the result of relaxed competing demands for flight maneuverability and takeoff ability in open water environments.

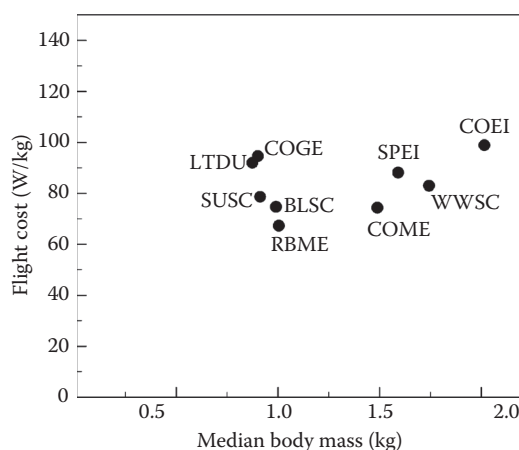


Figure 7.7. Flight costs of several sea duck species estimated using Flight software (Pennycuik 2008); parameters for calculations taken from Alerstam et al. (2007). BLSC, Black Scoter; COEI, Common Eider; COGO, Common Goldeneye; COME, Common Merganser; LTDU, Long-tailed Duck; RBME, Red-breasted Merganser; SUSC, Surf Scoter; SPEI, Spectacled Eider; and WWSC, White-winged Scoter.

Cost of Foraging

For diving birds, the energy costs of locating, pursuing, and capturing prey are complicated because they are obligated to return to the surface to breathe. Because sea ducks dive for their food, they must overcome the hydrodynamic drag associated with propelling the body through the water and the force of buoyancy while submerged (Lovvorn and Jones 1991, Lovvorn et al. 1991). As the duck descends in the water column, air in the respiratory system and plumage is compressed by hydrostatic pressure with increasing depth underwater, which then reduces the costs of countering the force of buoyancy. The drag force acting on a body increases rapidly with increasing speed (Hoerner 1958). These forces act in concert with other physiological limitations as a result of breath holding while exercising. Biomechanical models use measures of plumage volume, compression, and drag from live animals and specimens in tow tanks in concert with measures of oxygen consumption ($\text{mL O}_2/\text{s}$) to calculate aerobic efficiency during dives (Lovvorn et al. 1991b, 2004). We can then estimate costs of diving as a function of different depths. Interestingly, the costs of diving are not exceptionally higher than other activities such as flying or swimming (Lovvorn et al. 2009). Deep diving sea ducks often reach depths of over 10 m, where buoyancy becomes negligible and costs of underwater swimming are often lower than surface swimming and much lower than flying. In addition, thermal substitution may further offset energy costs for wing-propelled diving as waste heat generated from two large muscle masses in the breast and legs may also benefit the energy budget by reducing the costs of thermoregulation in cold water.

Diving is an essential part of foraging activity for sea ducks, but measuring the cost of diving for free-ranging birds is often complicated and challenging. Methods such as attaching data microloggers to birds or employing the doubly-labeled water technique require recapture of the same bird to measure metabolism, and cannot provide information on the cost of specific behaviors alone. Direct measures of metabolism using the dive-hole technique developed for penguins and seals in the Antarctic are not possible in most areas where sea ducks winter (Kooyman 1965). While there is great promise in the use of

heart-rate data loggers to obtain activity-specific metabolic rates (Butler et al. 1995), calibration for multiple species of differing body size is needed before this method can be used more broadly.

Observations of underwater swim mechanics further reveal details that allow sea ducks to minimize costs. With captive White-winged Scoters diving to 2 m in a tank, Richman and Lovvorn (2008) found that during descent birds used either foot propulsion alone or foot and wing propulsion simultaneously. Only foot strokes were used to resist the upward force of buoyancy while at the bottom, with the wings partially opened lateral to the body, which may increase drag to oppose buoyancy. Heath et al. (2006) described the stroke patterns of Common Eiders diving in the Canadian Arctic (Figure 7.8). Coordination of foot strokes and wing strokes may reduce overall drag by allowing more constant instantaneous speeds throughout the stroke cycle. During the upstroke, the wings had a fairly low angle of attack, whereas during the downstroke, and especially the transition between upstroke and downstroke, the angle of attack was much greater with presumably much higher drag. The recovery stroke, or retraction of the feet with the webbing closed, occurred during the upstroke of the wing, and the power stroke of the feet occurred during the transition of the wing stroke from upstroke to downstroke. This timing may avoid higher drag incurred by more unsteady thrust at the same mean speed, thereby reducing the energy cost of descent (Lovvorn 2001, Heath et al. 2006). Richman and Lovvorn (2008) further partitioned the energy cost of descent for White-winged Scoters, showing that the use of wings in addition to feet reduced the energy cost of descent by ~34%, which is an important advantage.

Thermoregulation

For shallow diving sea ducks, increased work rates to counter buoyancy near the surface may generate excess heat from exercising muscles, which may offset increased thermoregulatory demands of diving in cold water. However, optimal work rates during diving may change with decreasing water temperature. As thermostatic demands increase at lower water temperatures, heat loss may exceed metabolic heat production from exercise, and shivering begins (Lovvorn 2007).

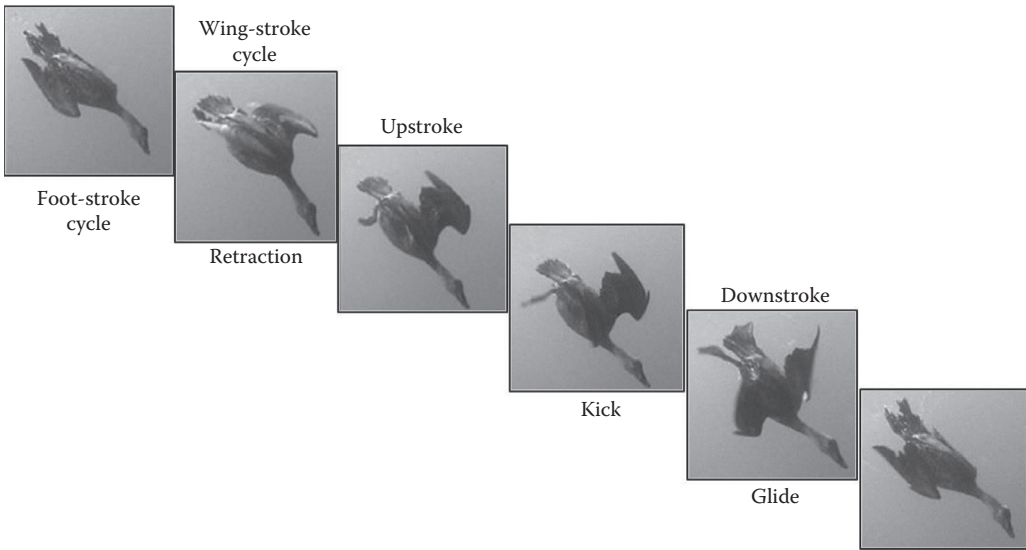


Figure 7.8. Wing- and foot-stroke cycles of the Common Eider diving at the Belcher Islands, Nunavut. (Photos from Heath et al. 2006.)

During exercise, threshold temperatures may set limits where heat loss exceeds metabolic heat production, which will affect an animal's foraging profitability as energy gain minus cost.

When discussing maintenance costs in the previous sections, we showed that thermoregulation can constitute a substantial part of all energy costs. The high thermostatic demands for diving birds can be met by (a) increasing metabolic heat production, (b) regional changes in blood flow and vasomotion, (c) allowing body temperature to decline, or (d) substitution from the heat generated by exercising muscles or digestion. There are both advantages and disadvantages to increasing metabolic heat production as it depletes oxygen stores quickly and requires higher energy intake.

Another important mechanism for thermoregulatory control in changes to blood flow, temporal variation in pulsatile blood flow to the legs, and overall reduction in body temperature during diving is to reduce heat loss and conserve oxygen by metabolic depression (Butler et al. 1995, Culik et al. 1996, Bevan et al. 1997, Handrich et al. 1997, de Leeuw et al. 1998); however, this is not a universal strategy. Some birds increase their body temperature during diving (Stephenson 1994), while others remain unchanged (Gallivan and Rolan 1979; Kaseloo and Lovvorn 2003, 2005). Variation in body temperature suggests that species of differing body mass and thermal inertia may use different strategies for

controlling heat loss and may use them in combination with other means of heat conservation.

Daily Energy Requirements and Allometry

Depending on a number of factors, we can calculate an animal's daily energy requirements (DER), which will guide estimates of the amount of food and thus amount of foraging habitat required. These calculations may appear straightforward, but their accuracy varies tremendously depending on what variables or parameter estimates are used in the calculations. The total energy requirement of an animal will change with environmental temperature throughout the day depending on the thermoregulatory capacity of the animal and will further increase with activity and during periods of growth, storage, and reproduction.

A convenient but perhaps oversimplified approach is to use allometric relationships between RMR and body mass to predict food requirements. One of the more common equations used is based on Miller and Eadie's (2006) analysis for waterfowl. However, data for diving ducks and particularly sea ducks are better described by allometric equations developed for seabirds (Ellis and Gabrielsen 2002). Richman and Lovvorn (2011) plotted RMR (W) in air and on water for diving ducks and found a linear relationship described by RMR_{air}

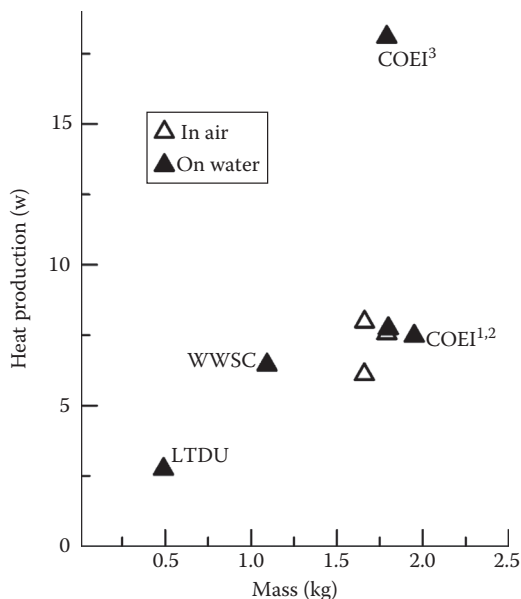


Figure 7.9. RMR (W) for sea ducks measured by open-flow respirometry in air and on water in relation to body mass (kg) (data from Table 7.2, Richman and Lovvorn 2011). COEI, Common Eider (¹Gabrielsen et al. 1991, ²Jenssen et al. 1989, ³Hawkins et al. 2000); WWSC, White-winged Scoter; and LTDU, Long-tailed Duck.

(W) = 3.83 mass (kg) + 0.67 ($R^2 = 0.94$, $P < 0.01$) and $RMR_{\text{water}} \text{ (W)} = 2.93 \text{ mass (kg)} + 2.37$ ($R^2 = 0.64$, $P < 0.01$, excluding Hawkins et al. 2000). For sea ducks, RMR (W) as a function of body mass is linear over a small range of body mass (Figure 7.9), but additional data is needed on metabolic rates of more sea duck species.

When converting RMR to DER, we must make several assumptions to correctly predict energy costs. Some models use detailed thermoregulatory costs and include balanced heat loss from the bird to the environment, which incorporate measures of ambient temperature and wind speed (McKinney and McWilliams 2005). This same model also incorporated estimates of the energy costs of specific daily activities of wintering waterfowl (Tables 7.1 and 7.2).

Threshold Prey Densities

The complement of different-sized predators that depend on a habitat must be able to meet their energy requirements at different levels of prey abundance. For example, when evaluating a habitat, it is important to consider the fraction of prey of different sizes or accessibility that are

effectively available to each predator (Werner 1979, Zwartz and Wanink 1984, Persson 1985, Dickman 1988). This principle is especially important when species of differing body size coexist in the same habitat. For example, larger species can search a larger area per unit time, eat greater amounts and broader size ranges of foods, and may be able to withstand prey depletion better than smaller predators restricted to smaller food items and thus a lower fraction of total food biomass (Schoener 1974, Gerritsen and Kou 1985, Goudie and Ankney 1986).

Measures of foraging profitability (energy gain minus cost) between different-sized predators can provide insight into the threshold prey density at which energy balance will switch from positive to negative. Richman and Lovvorn (2009) combined experimental measurements of dive costs and intake rates for small-bodied Lesser Scaup (*Aythya affinis*, ~600 g) and large-bodied White-winged Scoters (~1.2 kg). Using the energy intake equation (see the “Energy Intake” section), the authors incorporated seasonal variations in energy content, assimilation efficiency, size structure, and burial depth of prey and subtracted the costs of diving to assess the threshold prey densities for scaup versus scoters under different prey regimes. The authors showed that prey size and burial depth were important for determining threshold prey densities. In addition, the energy savings of using wing propulsion in addition to foot propulsion by scoters further reduced threshold prey densities by >10% (Richman and Lovvorn 2009). These variables would all have significant effects when scaled up to estimate the carrying capacity of a habitat for a combination of coexisting predators. Such analyses can provide information to estimate the carrying capacity of a particular habitat area for different species or, conversely, to estimate the habitat area required to support given populations of those species (Lovvorn et al. 2013). While some analyses have used allometric estimates of population density or area required for animals of a given body size (Silva and Downing 1994, Gaston and Blackburn 1996), others have estimated (also allometrically) the energy required by the predator population, and then compared that value to either the total biomass of food, or the biomass above some level of maximum profitable depletion (Korschgen et al. 1988, Michot 1997, Goss-Custard et al. 2003, Durell et al. 2006, Miller and Eadie 2006, Laursen et al. 2010). The approach

of comparing estimated energy requirements of mollusc-eating predators to the total standing stock of available food might lead to oversimplified understanding of complex natural ecosystems and mislead environmental management decisions. For example, shellfish management policy based on allometric estimates of bird energy demands has led to overexploitation of bivalve resources in the Netherlands, which resulted in food-shortages for mollusc-eating birds and mass mortality of Common Eiders (Camphuysen et al. 2002, Ens et al. 2004). For sea ducks, it appears that the threshold of maximum depletion or giving up density varies substantially with the size and associated depth distribution of their prey resource so that much less of the total standing stock of prey is profitably available to them.

We often assume that total prey density or biomass is a good measure of available foods. However, in conservation efforts, we urge consideration of the size and accessibility of prey in its value to all predators relying on these resources (Lovvorn et al. 2013). Not only must we measure the total amount of prey available (numerically as well as biomass), but we must also provide information of the size structure of that prey community. Not all prey is accessible or ingestible to all species of sea ducks, and total prey biomass is not equal to the functionally available prey biomass. It is important to consider these aspects on prey communities and predators, along with competitive interactions with other species; all of which can have major effects on our estimates of the numbers of different bird species an area of habitat can support.

Individual-Based Modeling

Sea duck habitat use, foraging ecology, and energetics are complex, and it can be challenging to synthesize the many component processes to understand their function and importance in population dynamics. Individual-based modeling (IBM) integrates multiple processes through simulation of actions and interactions of individuals (Goss-Custard et al. 1995a,b; Stillman et al. 2000; Grimm and Railsback 2005). IBMs are becoming increasingly popular in ecological research and have been used to answer a variety of questions about animal behavior, habitat use, bioenergetics, movements, and population dynamics. The key difference between IBMs and other modeling

techniques is that the characteristics of each individual animal are tracked through simulation time steps in an IBM, whereas characteristics of the population are averaged in other models. Conceptual frameworks of IBMs can be variable, but standard protocols have been proposed (Grimm et al. 2006). Several modeling platforms exist for creating IBMs, for example, NetLogo (Wilensky 1999) and MORPH (Stillman 2008), and some investigators choose to create their own IBM frameworks. There are only a few cases where IBMs have been applied to study ducks, but more examples are available from other taxonomic bird groups with similar ecology, such as shorebirds and geese (Duriez et al. 2009, Stillman and Goss-Custard 2010).

To answer questions about winter habitat requirements of Spectacled Eiders in light of changing food resources and climate change, Lovvorn et al. (2009) constructed an IBM integrating benthic prey dynamics over three decades and remotely sensed ice data into simulation models of bird energy balance. Simulation results showed that the area and distribution of the habitats of species foraging on sessile, benthic prey were dynamic on a decadal scale, and thus conservation efforts focused on managing fixed areas might be inadequate to protect such species. The modeling analysis and later applications revealed that loss of sea ice due to climate change could severely affect daily energy balance of Spectacled Eiders, which save energy by resting on ice instead of floating on water (Lovvorn et al. 2014).

Foraging ecology of Common Eiders wintering in the sea ice in Hudson Bay was modeled by Heath et al. (2010) by developing a dynamic state variable model, which could be considered a type of IBM. The authors built a set of behavioral-energetic models and through repeated simulations assessed a suite of environmental, behavioral, and physiological factors that influenced the energy budgets of wintering eiders affected by their foraging decisions (Heath and Gilchrist 2010, Heath et al. 2010). Heath et al. (2010) found that due to the strength and periodicity of currents, Common Eiders rested during the seemingly most profitable foraging period in slack currents but maximized their long-term energy intake by foraging in medium–strong current and digesting during slack currents.

Sea duck IBMs have also employed the MORPH platform (Stillman 2008). Kaiser et al. (2002) parameterized an IBM for Common Scoters

wintering in Liverpool Bay, United Kingdom, and simulated environmental impact scenarios to predict displacement of scoters from benthic-feeding areas due to offshore wind farms. Similarly, for Common Eiders wintering in the southern Baltic, a MORPH-based IBM was constructed to measure habitat carrying capacity under the baseline conditions and several impact scenarios of a fixed link construction (18 km long bridge or tunnel) between Denmark and Germany (Fehmarnbelt Fixed Link Bird Services 2013a,b). IBMs provide a useful way to integrate multiple ecological processes and analyze ecosystem-level questions, and these models will be more commonly used in sea duck research in the future.

FORAGING HABITAT REQUIREMENTS

Sea ducks use habitats with high prey density and environmental characteristics that minimize the energy costs of foraging. Common Eiders wintering in the Gulf of St. Lawrence aggregate over shallow patches with the highest prey density (Guillemette et al. 1993, Guillemette and Himmelman 1996). Where marine mussel farming is prevalent, sea ducks are attracted to the supplemental food source along migration routes or on wintering areas throughout the Pacific and Atlantic coasts of Canada, United States, and Europe (Ross and Furness 2000, Dionne et al. 2006, Kirk et al. 2007, Richman et al. 2012, Varennes et al. 2013). The phenomenon is similar to the attraction to waste corn as supplemental food for migrating waterfowl.

The distribution of Black Scoters wintering in Liverpool Bay, Irish Sea, UK, coincided with sites that had high abundance and biomass of bivalve prey; however, the scoters' distribution was also shaped by the shipping lanes, which scoters avoid (Kaiser et al. 2006). King Eiders and Common Eiders aggregate on habitat patches with the highest food densities in northern Norway and redistribute themselves over winter as prey is depleted (Bustnes et al. 2013). The use of habitats with high availability of suitable foods has been reported for other sea duck species in different regions (Žydellis and Ruškytė 2005; Kirk et al. 2007, 2008; Anderson and Lovvorn 2011; Fehmarnbelt Fixed Link Bird Services 2013a).

Furthermore, when different types of suitable prey are available within an area, sea ducks

clearly prefer habitat patches with higher-quality prey. Loring et al. (2013) found that higher densities of White-winged and Black Scoters wintering in Narragansett Bay, Rhode Island, are associated with mainly sandy-bottom infauna compared to mixed sediments with both infauna and epifauna, despite mixed sediments supporting higher total biomass of benthic organisms. The authors suggested that this pattern occurs because mixed bottoms contain firm sediments that are harder to penetrate and access infauna, which are the main prey for scoters in the area. In contrast, sand-substrate patches provide high-quality feeding habitat with more easily accessible prey. Similarly, Surf Scoters in Puget Sound use habitats where small mussels are abundant early in the wintering season and switch to sea grass habitats and a diet of crustaceans and gastropods in late winter, after mussels are depleted (Anderson and Lovvorn 2012).

Compelling evidence indicates that prey availability is often the most important factor determining sea duck habitat use. Depending on species and locality, other habitat features may also play an important role. Simultaneous consideration of multiple factors allows understanding of the relative importance of food versus other habitat characteristics. Distribution of Surf Scoters in San Francisco Bay was primarily influenced by the availability of herring roe, but other factors such as presence of eelgrass (*Zostera marina*), water depth, and salinity were also highly ranked in models explaining bird distribution (De La Cruz et al. 2014). In contrast, habitat use by Harlequin Ducks and Barrow's Goldeneyes in Prince William Sound, Alaska, was determined by landscape elements such as proximity to streams and shelter from wind and waves. Based on model selection, these variables were more important than prey biomass, suggesting that available food in that area likely well exceeds predation demands and that birds choose habitats that incur lower energy costs (Esler et al. 2000a,b). Sea duck habitat use may be viewed as a hierarchical phenomenon where birds distribute themselves according to general large-scale characteristics defining where species live (Johnson 1980), and then select patches offering the most available and accessible prey for harvest, balanced with the energy cost of obtaining that food.

CONCLUSIONS

Habitat-based conservation planning for sea ducks in the United States and Canada is guided by a philosophy outlined in the North American Waterfowl Management Plan (NAWMP) and implemented by regional Joint Ventures. Currently, the conservation plans developed by all NAWMP habitat Joint Ventures focused on migrating and wintering waterfowl are based on the premise that food is limiting; thus, increasing food abundance or habitats will result in improved demographic or physiological performance. To estimate habitat needs, we use bioenergetics models as a tool; however, model structure and inputs vary. Information needed to build bioenergetics models falls into two broad categories: energy availability on the landscape and energy needed by waterfowl species of interest. Over the past 20 years, we have seen considerable research directed at improving our understanding of both energy availability and energy requirements for sea ducks, but more information is needed to improve our science-based approach for achieving population objectives and habitat conservation.

ACKNOWLEDGMENTS

We are grateful to the editorial team for guidance, understanding, and support when writing this chapter, especially D. Derksen and V. Skean. Particularly instrumental were detailed reviews by M. Guillemain, S. R. McWilliams, and J. R. Lovvorn.

LITERATURE CITED

Alerstam, T., M. Rosén, J. Bäckman, P. G. P. Ericson, and O. Hellgren. 2007. Flight speeds among bird species: allometric and phylogenetic effects. *PLoS Biology* 5:e197.

Anderson, E. M., and J. R. Lovvorn. 2008. Gray whales may increase feeding opportunities for avian benthivores. *Marine Ecology Progress Series* 360:291–296.

Anderson, E. M., and J. R. Lovvorn. 2011. Contrasts in energy status and marine foraging strategies of White-winged Scoters (*Melanitta fusca*) and Surf Scoters (*M. perspicillata*). *Auk* 128:248–257.

Anderson, E. M., and J. R. Lovvorn. 2012. Seasonal dynamics of prey size mediate complementary functions of mussel beds and seagrass habitats for an avian predator. *Marine Ecology Progress Series* 467:219–232.

Anderson, E. M., J. R. Lovvorn, D. Esler, W. S. Boyd, and K. T. Stick. 2009. Using predator distributions, diet, and condition to evaluate seasonal foraging sites: sea ducks and herring spawn. *Marine Ecology Progress Series* 386:287–302.

Anderson, E. M., J. R. Lovvorn, and M. T. Wilson. 2008. Reevaluating marine diets of Surf and White-winged Scoters: interspecific differences and the importance of soft-bodied prey. *Condor* 110:285–295.

Bayne, B. L., and C. M. Worrall. 1980. Growth and production of mussels *Mytilus edulis* from two populations. *Marine Ecology Progress Series* 3:317–328.

Beauchamp, G. 1992. Diving behavior in Surf Scoters and Barrow's Goldeneyes. *Auk* 109:819–827.

Beauchamp, G., M. Guillemette, and R. Ydenberg. 1992. Prey selection while diving by Common Eiders, *Somateria mollissima*. *Animal Behaviour* 44:417–426.

Bevan, R. M., I. L. Boyd, P. J. Butler, K. Reid, A. J. Woakes, and J. P. Croxall. 1997. Heart rates and abdominal temperatures of free-ranging South Georgian Shags, *Phalacrocorax georgianus*. *Journal of Experimental Biology* 2000:661–675.

Bond, J. C., D. Esler, and K. A. Hobson. 2007. Isotopic evidence for sources of nutrients allocated to clutch formation by Harlequin Ducks. *Condor* 109:698–704.

Budge, S. M., S. W. Wang, T. E. Hollmén, and M. J. Wooller. 2011. Carbon isotopic fractionation in eider adipose tissue varies with fatty acid structure: implications for trophic studies. *Journal of Experimental Biology* 214:3790–3800.

Budge, S. M., M. J. Wooller, A. M. Springer, S. J. Iverson, C. P. McRoy, and G. J. Divoky. 2008. Tracing carbon flow in an arctic marine food web using fatty acid-stable isotope analysis. *Oecologia* 157:117–129.

Bustnes, J. O. 1998. Selection of blue mussels, *Mytilus edulis*, by Common Eiders, *Somateria mollissima*, by size in relation to shell content. *Canadian Journal of Zoology* 76:1787–1790.

Bustnes, J. O., and K. E. Erikstad. 1990. Size selection of common mussels, *Mytilus edulis*, by Common Eiders, *Somateria mollissima*: energy maximization or shell weight minimization? *Canadian Journal of Zoology* 68:2280–2283.

Bustnes, J. O., and O. J. Lonne. 1997. Habitat partitioning among sympatric wintering Common Eiders *Somateria mollissima* and King Eiders *Somateria spectabilis*. *Ibis* 139:549–554.

Bustnes, J. O., and G. H. Systad. 2001. Comparative feeding ecology of Steller's Eider and Long-tailed Ducks in winter. *Waterbirds* 24:407–412.

Bustnes, J. O., G. H. Systad, and R. C. Ydenberg. 2013. Changing distribution of flocking sea ducks as non-regenerating food sources are depleted. *Marine Ecology Progress Series* 484:249–257.

- Butler, P. J., R. M. Bevan, A. J. Woakes, J. P. Croxall, and I. L. Boyd. 1995. The use of data loggers to determine the energetics and physiology of aquatic birds and mammals. *Brazilian Journal of Medical and Biological Research* 28:1307–1317.
- Camphuysen, C. J., C. M. Berrevoets, H. J. W. M. Cremers, A. Dekinga, R. Dekker, B. J. Ens, T. M. van der Have, R. K. H. Kats, T. Kuiken, M. F. Leopold, J. van der Meer, and T. Piersma. 2002. Mass mortality of Common Eiders (*Somateria mollissima*) in the Dutch Wadden Sea, winter 1999/2000: starvation in a commercially exploited wetland of international importance. *Biological Conservation* 106:303–317.
- Culik, B. M., K. Putz, R. P. Wilson, D. Allers, J. Lage, C. A. Bost, and Y. Le Maho. 1996. Diving energetics in King Penguins (*Aptenodytes patagonicus*). *Journal of Experimental Biology* 199:973–983.
- De La Cruz, S. E. W., J. M. Eadie, A. K. Miles, J. Yee, K. A. Spragens, E. C. Palm, and J. Y. Takekawa. 2014. Resource selection and space use by sea ducks during the non-breeding season: implications for habitat conservation planning in urbanized estuaries. *Biological Conservation* 169:68–78.
- de Leeuw, J. J., P. J. Butler, A. J. Woakes, and F. Zegwaard. 1998. Body cooling and its energetic implications for feeding and diving of Tufted Ducks. *Physiological Zoology* 71:720–730.
- de Leeuw, J. J., and M. R. Van Eerden. 1992. Size selection in diving Tufted Ducks *Aythya fuligula* explained by differential handling of small and large mussels *Dreissena polymorpha*. *Ardea* 80:353–362.
- Dickman, C. R. 1988. Body size, prey size, and community structure in insectivorous mammals. *Ecology* 69:569–580.
- Dionne, M., J.-S. Lauzon-Guay, D. J. Hamilton, and M. A. Barbeau. 2006. Protective socking material for cultivated mussels: a potential non-disruptive deterrent to reduce losses to diving ducks. *Aquaculture International* 14:595–615.
- Dugger, B. D., K. M. Dugger, and L. H. Fredrickson. 2009. Hooded Merganser (*Lophodytes cucullatus*). in A. Poole (editor), *The Birds of North America*, No. 98. The Academy of Natural Sciences, Philadelphia, PA.
- Durell, S. E. A. I. V. d., R. A. Stillman, R. W. G. Caldow, S. McGorty, A. D. West, and J. Humphreys. 2006. Modelling the effect of environment change on shorebirds: a case study on Poole Harbour, UK. *Biological Conservation* 131:459–473.
- Duriez, O., S. Bauer, A. Destin., J. Madsen, B. A. Nolet, R. A. Stillman, and M. Klaassen. 2009. What decision rules might Pink-footed Geese use to depart on migration? An individual-based model. *Behavioral Ecology* 20:560–569.
- Ellis, H. I., and G. W. Gabrielsen. 2002. Energetics of free-ranging seabirds. Pp. 359–407 in E. A. Schreiber and J. Burger (editors), *Biology of Marine Birds*. CRC, Boca Raton, FL.
- Ens, B. J., A. C. Small, and J. de Vlas. 2004. The effects of shellfish fishery on the ecosystems of the Dutch Wadden Sea and Oosterschelde. Alterra-rapport 1011, Alterra, Wageningen, Netherlands.
- Esler, D., T. D. Bowman, T. A. Dean, C. E. O'Clair, S. C. Jewett, and L. L. McDonald. 2000a. Correlates of Harlequin Duck densities during winter in Prince William Sound, Alaska. *Condor* 102:920–926.
- Esler, D., T. D. Bowman, C. E. O'Clair, T. A. Dean, and L. L. McDonald. 2000b. Densities of Barrow's Goldeneyes in Prince William Sound, Alaska in relation to food, habitat and history of oil contamination. *Waterbirds* 23:423–429.
- Fehmarnbelt Fixed Link Bird Services. [online]. 2013a. Fehmarnbelt fixed link EIA. Bird investigations in Fehmarnbelt—baseline (vol. II). *Waterbirds in Fehmarnbelt*. Report No. E3TR0011. <<http://vmdocumentation.femern.com/>> (1 April 2014).
- Fehmarnbelt Fixed Link Bird Services. [online]. 2013b. Fehmarnbelt fixed link EIA. Fauna and Flora—impact assessment—Birds of the Fehmarnbelt area. Report No. E3TR0015. <<http://vmdocumentation.femern.com/>> (1 April 2014).
- Fox, A. D., and C. Mitchell. 1997. Spring habitat use and feeding behavior of Steller's Eider *Polysticta stelleri* in Varangerfjord, northern Norway. *Ibis* 139:542–548.
- Gabrielsen, G. W., F. Mehlum, H. E. Karlsen, O. Andresen, and H. Parker. 1991. Energy cost during incubation and thermoregulation in the female Common Eider *Somateria mollissima*. *Norsk Polarinstitut Skrifter* 195:51–62.
- Gallivan, G. J., and K., Roland. 1979. Temperature regulation in freely diving harp seals (*Phoca groenlandica*). *Canadian Journal of Zoology* 57:2256–2263.
- Gaston, K. J., and T. M. Blackburn. 1996. Conservation implications of geographic range size-body size relationships. *Conservation Biology* 10:638–646.
- Gauthier, G. 1993. Bufflehead (*Bucephala albeola*). in A. Poole and F. Gill (editors), *The Birds of North America*, No. 67. The Academy of Natural Sciences, Philadelphia, PA.
- Gauthier, G., J. Betty, and K. A. Hobson. 2003. Are Greater Snow Geese capital breeders? New evidence from a stable-isotope model. *Ecology* 84:3250–3264.
- Gerritsen, J., and J.-I. Kou. 1985. Food limitation and body size. *Archiv fur Hydrobiologie Beiheft Ergebnisse der Limnologie* 21:173–184.

- Goss-Custard, J. D., R. W. G. Caldow, R. T. Clarke, S. E. A. I. V. d. Durell, and W. J. Sutherland. 1995a. Deriving population parameters from individual variations in foraging behaviour. 1. Empirical game-theory distribution model of Oystercatchers *Haematopus ostralegus* feeding on mussels *Mytilus edulis*. *Journal of Animal Ecology* 64:265–276.
- Goss-Custard, J. D., R. W. G. Caldow, R. T. Clarke, and A. D. West. 1995b. Deriving population parameters from individual variations in foraging behavior. 2. Model tests and population parameters. *Journal of Animal Ecology* 64:277–289.
- Goss-Custard, J. D., R. A. Stillman, R. W. G. Caldow, A. D. West, and M. Guillemain. 2003. Carrying capacity in overwintering birds: when are spatial models needed? *Journal of Animal Ecology* 40:176–187.
- Goudie, R. I. 1999. Behaviour of Harlequin Ducks and three species of scoters wintering in the Queen Charlotte Islands, British Columbia. in R. I. Goudie, M. R. Petersen, and G. J. Robertson (editors), *Behaviour and ecology of sea ducks*. Occasional Paper, No. 100. Canadian Wildlife Service, Environment Canada, Ottawa, ON.
- Goudie, R. I., and C. D. Ankney. 1986. Body size, activity budgets, and diets of sea ducks wintering in Newfoundland. *Ecology* 67:1475–1482.
- Grimm, V., U. Berger, F. Bastiansen, S. Eliassen, V. Ginot, J. Giske, J. Goss-Custard et al. 2006. A standard protocol for describing individual-based and agent-based models. *Ecological Modelling* 198:115–126.
- Grimm, V., and S. F. Railsback. 2005. *Individual-based modeling and ecology*. Princeton University Press, Princeton, NJ.
- Guillemette, M. 1994. Digestive-rate constraint in wintering Common Eiders (*Somateria mollissima*): implications for flying capabilities. *Auk* 111:900–909.
- Guillemette, M. 1998. The effect of time and digestion constraints in Common Eiders while feeding and diving over blue mussel beds. *Functional Ecology* 12:123–131.
- Guillemette, M. 2001. Foraging before spring migration and before breeding in Common Eiders: does hyperphagia occur? *Condor* 103:633–638.
- Guillemette, M., and J. H. Himmelman. 1996. Distribution of wintering Common Eiders over mussel beds: does the ideal free distribution apply? *Oikos* 76:435–442.
- Guillemette, M., J. H. Himmelman, C. Barette, and A. Reed. 1993. Habitat selection by Common Eiders in winter and its interaction with flock size. *Canadian Journal of Zoology* 71:1259–1266.
- Guillemette, M., R. C. Ydenberg, and J. H. Himmelman. 1992. The role of energy intake rate in prey and habitat selection of Common Eiders *Somateria mollissima* in winter: a risk-sensitive interpretation. *Journal of Animal Ecology* 61:599–610.
- Hamilton, D. J., T. D. Nudds, and J. Neate. 1999. Size-selective predation of blue mussels (*Mytilus edulis*) by Common Eiders (*Somateria mollissima*) under controlled field conditions. *Auk* 116:403–416.
- Handrich, Y., R. M. Bevan, J.-B. Charrassin, P. J. Butler, K. Ptz, A. J. Woakes, J. Lage, and Y. Le Maho. 1997. Hypothermia in foraging King Penguins. *Nature* 388:64–67.
- Hario, M., and M. Öst. 2002. Does heavy investment in foraging implicate low food acquisition for female Common Eider *Somateria mollissima*? *Ornis Fennica* 79:111–120.
- Hawkins, P. A. J., P. J. Butler, A. J. Woakes, and J. R. Speakman. 2000. Estimation of the rate of oxygen consumption of the Common Eider duck (*Somateria mollissima*), with some measurements of heart rate during voluntary dives. *Journal of Experimental Biology* 203:2819–2832.
- Heath, J. P., and H. G. Gilchrist. 2010. When foraging becomes unprofitable: energetics of diving in tidal currents by Common Eiders wintering in the Arctic. *Marine Ecology Progress Series* 403:279–290.
- Heath, J. P., H. G. Gilchrist, and R. C. Ydenberg. 2006. Regulation of stroke pattern and swim speed across a range of current velocities: diving by Common Eiders wintering in the Canadian Arctic. *Journal of Experimental Biology* 209:3974–3983.
- Heath, J. P., H. G. Gilchrist, and R. C. Ydenberg. 2007. Can dive cycle models predict patterns of foraging behavior? Diving by Common Eiders in an Arctic polynya. *Animal Behaviour* 73:877–884.
- Heath, J. P., H. G. Gilchrist, and R. C. Ydenberg. 2010. Interactions between rate processes with different timescales explain counterintuitive foraging patterns of arctic wintering eiders. *Proceedings of the Royal Society B* 277:3179–3186.
- Hepp, G. R., R. J. Blohm, R. E. Reynolds, J. E. Hines, and J. D. Nichols. 1986. Physiological condition of autumn-banded Mallards and its relationship to hunting vulnerability. *Journal of Wildlife Management* 50:177–183.
- Hobson, K. A. 2006. Using stable isotopes to quantitatively track endogenous and exogenous nutrient allocations to eggs of birds that travel to breed. *Ardea* 94:359–369.
- Hoerner, S. F. 1958. Fluid dynamic drag: practical information on aerodynamic and hydrodynamic resistance. Hoerner Fluid Dynamics, Bricktown, NJ.
- Iverson, S. J., C. Field, W. Don Bowen, and W. Blanchard. 2004. Quantitative fatty acid signature analysis: a new method of estimating predator diets. *Ecological Monographs* 74:211–235.

- Jenssen, B. M., and M. Ekker. 1989. Thermoregulatory adaptations to cold in winter-acclimatized Long-tailed Ducks (*Clangula hyemalis*). Pp. 147–152 in C. Bech and R. E. Reinertsen (editors), *Physiology of Cold Adaptation in Birds*. Plenum, New York.
- Jenssen, B. M., and M. Ekker. 1991. Effects of plumage contamination with crude oil dispersant mixtures on thermoregulation in Common Eiders and Mallards. *Archives of Environmental Contamination and Toxicology* 20:398–403.
- Jenssen, B. M., M. Ekker, and C. Bech. 1989. Thermoregulation in winter-acclimatized Common Eiders (*Somateria mollissima*) in air and water. *Canadian Journal of Zoology* 67:669–673.
- Jeschke, J. M., M. Kopp, and R. Tollrian. 2002. Predator functional responses: discriminating between handling and digesting prey. *Ecological Monographs* 72:95–112.
- Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61:65–71.
- Kaiser, M. J., A. J. Elliott, M. Galanidi, E. I. S. Rees, R. W. G. Caldow, R. A. Stillman, W. J. Sutherland, and D. A. Showler. 2002. Predicting the displacement of Common Scoter *Melanitta nigra* from benthic feeding areas due to offshore windfarms. University of Wales Bangor Report to COWRIE, Bangor, U.K.
- Kaiser, M. J., M. Galanidi, D. A. Showler, A. J. Elliott, R. W. G. Caldow, E. I. S. Rees, R. A. Stillman, and W. J. Sutherland. 2006. Distribution and behaviour of Common Scoter *Melanitta nigra* relative to prey resources and environmental parameters. *Ibis* 148:110–128.
- Kasello, P. A., and J. R. Lovvorn. 2003. Heat increment of feeding and thermal substitution in Mallard ducks feeding voluntarily on grain. *Journal of Comparative Physiology B* 173:207–213.
- Kasello, P. A., and J. R. Lovvorn. 2005. Effects of surface activity patterns and dive depth on thermal substitution in fasted and fed Lesser Scaup ducks. *Canadian Journal of Zoology* 83:301–311.
- Kautsky, N. 1982. Quantitative studies on gonad cycle, fecundity, reproductive output and recruitment in a Baltic *Mytilus edulis* population. *Marine Biology* 68:143–160.
- Kautsky, N., K. Johannesson, and M. Tedengren. 1990. Genotypic and phenotypic differences between Baltic and North Sea populations of *Mytilus edulis* evaluated through reciprocal transplantations. I. Growth and morphology. *Marine Ecology Progress Series* 59:203–210.
- Kersten, M., and T. Piersma. 1987. High levels of energy expenditure in shorebirds; metabolic adaptations to an energetically expensive way of life. *Ardea* 75:175–187.
- Kestenholz, M. 1994. Body mass dynamics of wintering Tufted Duck *Aythya fuligula* and Pochard *A. ferina* in Switzerland. *Wildfowl* 45:147–158.
- Kirk, M., D. Esler, and W. S. Boyd. 2007. Morphology and density of mussels on natural and aquaculture structure habitats: implication for sea duck predators. *Marine Ecology Progress Series* 346:179–187.
- Kirk, M., D. Esler, S. A. Iverson, and W. S. Boyd. 2008. Movements of wintering Surf Scoters: predator responses to different prey landscapes. *Oecologia* 155:859–867.
- Kleiber, M. 1932. Body size and metabolism. *Hilgardia* 6:315–353.
- Kooyman, G. L. 1965. Techniques used in measuring diving capacities of Weddell Seals. *Polar Record* 12:391–394.
- Korschgen, C. E., L. S. George, and W. L. Green. 1988. Feeding ecology of Canvasbacks staging on Pool 7 of the upper Mississippi River. Pp. 237–249 in M. W. Weller (editor), *Waterfowl in winter*. University of Minnesota Press, Minneapolis, MN.
- Kristjánsson, T. Ö., J. E. Jónsson, and J. Svavarsson. 2013. Spring diet of Common Eiders (*Somateria mollissima*) in Breiðafjörður, West Iceland, indicates non-bivalve preferences. *Polar Biology* 36:51–59.
- Lacroix, D. L., S. Boyd, D. Esler, M. Kirk, T. Lewis, and S. Lipovsky. 2005. Surf Scoters *Melanitta perspicillata* aggregate in association with ephemerally abundant polychaetes. *Marine Ornithology* 33:61–63.
- Laubhan, M. K., and K. A. Metzner. 1999. Distribution and diurnal behavior of Steller's Eiders wintering on the Alaska Peninsula. *Condor* 101:694–698.
- Laursen, K., P. S. Kristensen, and P. Clausen. 2010. Assessment of blue mussel *Mytilus edulis* fisheries on waterbird shellfish-predator management in the Danish Wadden Sea. *Ambio* 39:476–485.
- Leopold, M. F., A. Cervencel, and F. Müller. 2012. Eidereend *Somateria mollissima* eet vis (Fish-eating eider). *Sula* 45:41–44.
- Lewis, T. L., D. Esler, and W. S. Boyd. 2007a. Effects of predation by sea ducks on clam abundance in soft-bottom intertidal habitats. *Marine Ecology Progress Series* 329:131–144.
- Lewis, T. L., D. Esler, and W. S. Boyd. 2007b. Foraging behaviors of Surf Scoters and White-winged Scoters during spawning of Pacific herring. *Condor* 109:216–222.
- Lewis, T. L., D. Esler, and W. S. Boyd. 2008. Foraging behavior of Surf Scoters (*Melanitta perspicillata*) and White-winged Scoters (*M. fusca*) in relation to clam density: inferring food availability and habitat quality. *Auk* 125:149–157.
- Lewis, T. L., D. Esler, W. S. Boyd, and R. Žydelsis. 2005. Nocturnal foraging behavior of wintering Surf Scoters and White-winged Scoters. *Condor* 107:637–647.

- Lok, E. K., D. Esler, J. Y. Takekawa, S. De La Cruz, W. S. Boyd, D. R. Nysewander, J. R. Evenson, and D. H. Ward. 2012. Spatiotemporal associations between Pacific herring and Surf Scoter spring migration: evaluating a 'silver wave' hypothesis. *Marine Ecology Progress Series* 457:139–150.
- Loring, P. H., P. W. P. Paton, S. R. McWilliams, R. A. McKinney, and C. A. Oviatt. 2013. Densities of wintering scoters in relation to benthic prey assemblages in a North Atlantic estuary. *Waterbirds* 36:144–155.
- Lovvorn, J. R. 2001. Upstroke thrust, drag effects, and stroke-glide cycles in wing-propelled swimming by birds. *American Zoologist* 41:154–165.
- Lovvorn, J. R. 2007. Thermal substitution and aerobic efficiency: measuring and predicting effects of heat balance on endotherm diving energetics. *Philosophical Transactions of the Royal Society of London B* 362:2079–2093.
- Lovvorn, J. R., E. M. Anderson, A. R. Rocha, W. W. Larned, J. M. Grebmeier, L. W. Cooper, J. M. Kolts, and C. A. North. 2014. Variable wind, pack ice, and prey dispersion affect the long-term adequacy of protected areas for an Arctic sea duck. *Ecological Applications* 24:396–412.
- Lovvorn, J. R., S. E. De La Cruz, J. W. Takekawa, L. E. Shaskey, and S. E. Richman. 2013. Niche overlap, threshold food densities, and limits to prey depletion for a diving duck assemblage in an estuarine bay. *Marine Ecology Progress Series* 476:251–268.
- Lovvorn, J. R., J. M. Grebmeier, L. W. Cooper, J. K. Bump, and S. E. Richman. 2009. Modelling marine protected area for threatened eiders in a climatically changing Bering Sea. *Ecological Applications* 19:1596–1613.
- Lovvorn, J. R., and D. R. Jones. 1991. Body mass, volume, and buoyancy of some aquatic birds, and their relation to locomotor strategies. *Canadian Journal of Zoology* 69:2888–2892.
- Lovvorn, J. R., and D. R. Jones. 1994. Biomechanical conflicts between diving and aerial flight in estuarine birds. *Estuaries* 17:62–75.
- Lovvorn, J. R., D. R. Jones, and R. W. Blake. 1991. Mechanics of underwater locomotion in diving ducks: drag, buoyancy, and acceleration in a size gradient of species. *Journal of Experimental Biology* 159:89–108.
- Lovvorn, J. R., S. E. Richman, J. M. Grebmeier, and L. W. Cooper. 2003. Diet and body condition of Spectacled Eiders wintering in pack ice of the Bering Sea. *Polar Biology* 26:259–267.
- Lovvorn, J. R., Y. Watanuki, A. Kato, Y. Naito, and G. A. Liggins. 2004. Stroke patterns and regulation of swim speed and energy cost in free-ranging Brünnich's Guillemots. *Journal of Experimental Biology* 207:4679–4695.
- MacArthur, R. H., and E. R. Pianka. 1966. On the optimal use of a patchy environment. *American Naturalist* 100:603–609.
- Mallory, M., and K. Metz. 1999. Common Merganser (*Mergus merganser*). in A. Poole and F. Gill (editors), *The Birds of North America*, No. 442. The Academy of Natural Sciences, Philadelphia, PA.
- McKinney, R. A., and S. R. McWilliams. 2005. A new model to estimate daily energy expenditure for wintering waterfowl. *Wilson Bulletin* 117:44–55.
- McNeil, R., P. Drapeau, and J. D. Goss-Custard. 1992. The occurrence and adaptive significance of nocturnal habits in waterfowl. *Biological Reviews* 67:381–419.
- McWilliams, S. R., and W. H. Karasov. 2001. Phenotypic flexibility in digestive system structure and function in migratory birds and its ecological significance. *Comparative Biochemistry and Physiology A* 128:579–593.
- Merkel, F. R., S. E. Jamieson, K. Falk, and A. Mosbech. 2007. The diet of Common Eiders wintering in Nuuk, Southwest Greenland. *Polar Biology* 30:227–234.
- Merkel, F. R., and A. Mosbech. 2008. Diurnal and nocturnal feeding strategies in Common Eiders. *Waterbirds* 31:580–586.
- Michot, T. C. 1997. Carrying capacity of seagrass beds predicted for Redheads wintering in Chandeleur Sound, Louisiana, USA. Pp. 93–102 in J. Goss-Custard, R. Rufino, and A. Luis (editors), *Effect of habitat loss and change on waterbirds*. Wetlands International Publication No. 42. The Stationery Office, London, U.K.
- Miller, M. R., and J. M. Eadie. 2006. The allometric relationship between resting metabolic rate and body mass in wild waterfowl (Anatidae) and an application to estimation of winter habitat requirements. *Condor* 108:166–177.
- Mosbech, A., R. S. Danø, F. Merkel, C. Sonne, G. Gilchrist, and A. Flagstad. 2006. Use of satellite telemetry to locate key habitats for King Eiders *Somateria spectabilis* in West Greenland. Pp. 769–776 in G. C. Boere, C. A. Galbraith, and D. A. Stroud (editors), *Waterbirds around the world*. The Stationery Office, Edinburgh, U.K.
- Navarro, R. A., C. R. Velasquez, and R. P. Schlatter. 1989. Diet of the surfbird in southern Chile. *Wilson Bulletin* 101:137–141.
- Nehls, G. 1995. Strategien der ernährung und ihre bedeutung für energiehaushalt und ökologie der Eiderente (*Somateria mollissima* (L., 1758)). Dissertation, Kiel University, Kiel, Germany (in German).
- Nilsson, L. 1970. Food-seeking activity of south Swedish diving ducks in the non-breeding season. *Oikos* 21:145–154.

- Ouellet, J.-F., C. Vanpe, and M. Guillemette. 2013. The body size-dependent diet composition of North American sea ducks in winter. *PLoS One* 8:e65667.
- Oppel, S., A. N. Powell, and M. G. Butler. 2011. King Eider foraging effort during the pre-breeding period in Alaska. *Condor* 113:52-60.
- Owen, M. 1990. Nocturnal feeding in waterfowl. *Acta XXth Congressus Internationalis Ornithologici* 2:1105-1112.
- Palm, E. C., D. Esler, E. M. Anderson, T. D. Williams, and M. T. Wilson. 2013. Variation in physiology and energy management of wintering White-winged Scoters in relation to local habitat conditions. *Condor* 115:750-761.
- Pelletier, D., M. Guillemette, J. M. Grandbois, and P. J. Butler. 2007. It is time to move: linking flight and foraging behavior in a diving bird. *Biology Letters* 3:357-359.
- Pelletier, D., M. Guillemette, J.-M. Grandbois, and P. J. Butler. 2008. To fly or not to fly: high costs in a large sea duck do not imply an expensive lifestyle. *Proceedings of the Royal Society B* 275:2117-2124.
- Pennycuik, C. J. 2008. *Modelling the flying bird*. Elsevier, Burlington, MA.
- Perry, M. C. 2012. Foraging behavior of Long-tailed Ducks in a ferry wake. *Northeastern Naturalist* 19:135-139.
- Persson, L. 1985. Asymmetric competition: are larger animals competitively superior? *American Naturalist* 126:261-266.
- Petersen, M. 1980. Observations of wing-feather moult and summer feeding ecology of Steller's Eiders at Nelson Lagoon, Alaska. *Wildfowl* 31:99-106.
- Peterson, S. R., and R. S. Ellarson. 1979. Changes in Oldsquaw weight. *Wilson Bulletin* 91:288-300.
- Pierce, G. J., and J. G. Ollason. 1987. Eight reasons why optimal foraging theory is a complete waste of time. *Oikos* 49:111-117.
- Powell, A. N., and R. S. Suydam. 2012. King Eider (*Somateria spectabilis*). in A. Poole and F. Gill (editors), *The Birds of North America*, No. 547. The Academy of Natural Sciences, Philadelphia, PA.
- Pyke, G. H. 1984. Optimal foraging theory: a critical review. *Annual Review of Ecology and Systematics* 15:523-575.
- Richman, S. E., and J. R. Lovvorn. 2003. Effects of clam species dominance on nutrient and energy acquisition by Spectacled Eiders in the Bering Sea. *Marine Ecology Progress Series* 261:283-297.
- Richman, S. E., and J. R. Lovvorn. 2004. Relative foraging value to Lesser Scaup ducks of native and exotic clams from San Francisco Bay. *Ecological Applications* 14:1217-1231.
- Richman, S. E., and J. R., Lovvorn. 2008. Cost of diving by wing and foot propulsion in a sea duck, the White-winged Scoter. *Journal of Comparative Physiology B* 178:321-332.
- Richman, S. E., and J. R. Lovvorn. 2009. Predator size, prey size and threshold food densities of diving ducks: does a common prey base support fewer large animals? *Journal of Animal Ecology* 78:1033-1042.
- Richman, S. E., and J. R. Lovvorn. 2011. Effects of air and water temperatures on resting metabolism of auklets and other diving birds. *Physiological and Biochemical Zoology* 84:316-332.
- Richman, S. E., E. Varennes, J. Bonadelli, and M. Guillemette. 2012. Sea duck predation on mussel farms: growing conflict. *Proceedings of Aquaculture Canada*, Quebec City, QC.
- Rigou, Y., and M. Guillemette. 2010. Foraging effort and pre-laying strategy in breeding Common Eiders. *Waterbirds* 33:314-322.
- Rizzolo, D. J., D. Esler, D. D. Roby, and R. L. Jarvis. 2005. Do wintering Harlequin Ducks forage nocturnally at high latitudes? *Condor* 107:173-177.
- Rodway, M. S. 2003. Timing of pairing in Harlequin Ducks: interaction of spacing behaviour, time budgets, and the influx of herring spawn. Doctoral dissertation, Simon Fraser University, Burnaby, BC.
- Ross, B. P., and R. W. Furness. 2000. Minimizing the impact of eider ducks on mussel farming. *Ornithology Group*, University of Glasgow, Glasgow, Scotland.
- Rumohr, H., T. Brey, and S. Ankar. 1987. A compilation of biometric conversion factors for benthic invertebrates of the Baltic Sea. *Baltic Marine Biologists Publication* 9:1-56.
- Schamber, J. L., D. Esler, and P. L. Flint. 2009. Evaluating the validity of using unverified indices of body condition. *Journal of Avian Biology* 40:49-56.
- Schenkeveld, L. E., and R. C. Ydenberg. 1985. Synchronous diving by Surf Scoter flocks. *Canadian Journal of Zoology* 63:2516-2519.
- Schmidt-Nielsen, K. 1975. *Animal physiology. Adaptation and environment*. Cambridge University Press, London, U.K.
- Schmutz, J. A., K. A. Hobson, and J. A. Morse. 2006. An isotopic assessment of protein from diet and endogenous stores: effect on egg production and incubation behaviour of geese. *Ardea* 94:385-397.
- Schoener, T. W. 1974. Resource partitioning in ecological communities. *Science* 185:27-39.
- Schorger, A. W. 1947. The deep diving of the Loon and Old-squaw and its mechanism. *Wilson Bulletin* 59:151-159.

- Schreer, J. F., and K. M. Kovacs. 1997. Allometry of diving capacity in air-breathing vertebrates. *Canadian Journal of Zoology* 75:339–358.
- Schummer, M. L., S. A. Petrie, A. M. Bailey, and S. S. Badzinski. 2012. Factors affecting lipid reserves and foraging activity of Buffleheads, Common Goldeneyes, and Long-tailed Ducks during winter at Lake Ontario. *Condor* 114:62–74.
- Silva, M., and J. A. Downing. 1994. Allometric scaling of minimal mammal densities. *Conservation Biology* 8:732–743.
- Stempniewicz, L. 1995. Feeding ecology of the Long-tailed Duck *Clangula hyemalis* wintering in the Gulf of Gdansk (southern Baltic Sea). *Ornis Svecica* 5:133–142.
- Stephens, D. W., J. S. Brown, and R. C. Ydenberg. 2007. *Foraging behavior and ecology*. Chicago University Press, Chicago, IL.
- Stephenson, R. 1994. Diving energetics in Lesser Scaup (*Aythya affinis*, Eyton). *Journal of Experimental Biology* 190:155–178.
- Stillman, R. A. 2008. MORPH—an individual-based model to predict the effect of environmental change on foraging animal populations. *Ecological Modelling* 216:265–276.
- Stillman, R. A., and J. D. Goss-Custard. 2010. Individual-based ecology of coastal birds. *Biological Reviews* 85:413–434.
- Stillman, R. A., J. D. Goss-Custard, A. D. West, S. E. A. I. V. d. Durell, R. W. G. Caldow, S. McGrorty, and R. T. Clarke. 2000. Predicting mortality in novel environments: tests and sensitivity of a behaviour-based model. *Journal of Applied Ecology* 37:564–588.
- Systad, G. H., and J. O. Bustnes. 2001. Coping with darkness and low temperatures: foraging strategies in Steller's Eiders, *Polysticta stelleri*, wintering at high latitudes. *Canadian Journal of Zoology* 79:402–406.
- Systad, G. H., J. O. Bustnes, and K. E. Erikstad. 2000. Behavioral responses to decreasing day length in wintering sea ducks. *Auk* 117:33–40.
- Titman, R. D. 1999. Red-breasted Merganser (*Mergus serrator*). in A. Poole and F. Gill (editors), *The Birds of North America*, No. 443. The Academy of Natural Sciences, Philadelphia, PA.
- VanStratt, C. S. 2011. Foraging effort by Surf Scoter at the peripheries of their wintering distribution: do foraging conditions influence their range? Thesis. Simon Fraser University, Burnaby, BC.
- Vareannes, É., S. A. Hanssen, J. Bonardelli, and M. Guillemette. 2013. Sea duck predation in mussel farms: the best nets for excluding Common Eiders safely and efficiently. *Aquaculture Environment Interactions* 4:31–39.
- Waldeck, P., and K. Larsson. 2013. Effects of winter water temperature on mass loss in Baltic blue mussels: implications for foraging sea ducks. *Journal of Experimental Marine Biology and Ecology* 444:24–30.
- Wang, S. W., T. E. Hollmén, and S. J. Iverson. 2010. Validating quantitative fatty acid signature analysis to estimate diets of Spectacled and Steller's Eiders (*Somateria fischeri* and *Polysticta stelleri*). *Journal of Comparative Physiology B—Biochemical, Systemic, and Environmental Physiology* 180:125–139.
- Werner, E. E. 1979. Niche partitioning by food size in fish communities. Pp. 311–322 in H. Clepper (editor), *Predator-prey systems in fisheries management*. Sport Fishing Institute, Washington, DC.
- White, T. P. 2013. Spatial ecology of Long-tailed Ducks and White-winged Scoters wintering on Nantucket Shoals, Massachusetts. Ph.D. thesis, City University of New York, New York, NY.
- White, T. P., R. R. Veit, and M. C. Perry. 2009. Feeding ecology of Long-tailed Ducks *Clangula hyemalis* wintering on the Nantucket Shoals. *Waterbirds* 32:293–299.
- Wilensky, U. [online]. 1999. NetLogo. Center for connected learning and computer-based modeling. Northwestern University, Evanston, IL. <<http://ccl.northwestern.edu/netlogo/>> (1 April 2014).
- Ydenberg, R. C. 1988. Foraging by diving birds. *Proceedings of the XIXth International Ornithological Congress* 9:1832–1842.
- Zwarts, L., and J. H. Wanink. 1984. How Oystercatchers and Curlews successively deplete clams. Pp. 69–83 in P. R. Evans, J. D. Goss-Custard, and W. G. Hale (editors), *Coastal waders and wildfowl in winter*. Cambridge University Press, Cambridge, U.K.
- Zwarts, L., and J. H. Wanink. 1993. How the food supply harvestable by waders in the Wadden Sea depends on the variation in energy density, body weight, biomass, burying depth and behaviour of tidal-flat invertebrates. *Netherlands Journal of Sea Research* 31:441–476.
- Žydels, R., and D. Esler. 2005. Response of wintering Steller's Eiders to herring spawn. *Waterbirds* 28:344–350.
- Žydels, R., and D. Ruškytė. 2005. Winter foraging of Long-tailed Ducks (*Clangula hyemalis*) exploiting different benthic communities in the Baltic Sea. *Wilson Bulletin* 117:133–141.

