# Estimating habitat carrying capacity for migrating and wintering waterfowl: considerations, pitfalls and improvements

CHRISTOPHER K. WILLIAMS[1]*, BRUCE D. DUGGER[2],
MICHAEL G. BRASHER[3], JOHN M. COLUCCY[4], DANE M. CRAMER[4],
JOHN M. EADIE[5], MATTHEW J. GRAY[6], HEATH M. HAGY[7],
MARK LIVOLSI[1], SCOTT R. McWILLIAMS[8], MARK PETRIE[9],
GREGORY J. SOULLIERE[10], JOHN M. TIRPAK[11] &
ELISABETH B. WEBB[12]

[1]Department of Entomology and Wildlife Ecology, University of Delaware,
250 Townsend Hall, Newark, Delaware 19716, USA.
[2]Department of Fisheries and Wildlife, Oregon State University, Corvallis, Oregon 97331, USA.
[3]Ducks Unlimited, Inc., Gulf Coast Joint Venture, 700 Cajundome Blvd, Lafayette,
Louisiana 70506, USA.
[4]Ducks Unlimited, Inc., Great Lakes/Atlantic Region, 1220 Eisenhower Place, Ann Arbor,
Michigan 48108, USA.
[5]Department of Wildlife, Fish and Conservation Biology, University of California,
1 Shields Avenue, Davis, California 95616, USA.
[6]Department of Forestry, Wildlife and Fisheries, University of Tennessee,
274 Ellington Plant Sciences Building, Knoxville, Tennessee 37996, USA.
[7]Forbes Biological Station – Bellrose Waterfowl Research Center, Illinois
Natural History Survey, University of Illinois at Urbana-Champaign, P.O. Box 590,
Havana, Illinois 62644, USA.
[8]Department of Natural Resources Science, University of Rhode Island,
105 Coastal Institute, Kingston, Rhode Island 02881, USA.
[9]Ducks Unlimited Inc. Western Regional Office, 17800 SE Mill Plain Blvd. Suite 120,
Vancouver, Washington 98683, USA.
[10]U.S. Fish and Wildlife Service, Upper Mississippi River and Great Lakes Region
Joint Venture Science Office, 2651 Coolidge Road, Suite 101, East Lansing,
Michigan 48823, USA.
[11]U.S. Fish and Wildlife Service, Gulf Coastal Plains & Ozarks Landscape Conservation
Cooperative, 700 Cajundome Blvd, Lafayette, Louisiana 70506, USA.
[12]U.S. Geological Survey, Missouri Cooperative Fish and Wildlife Research Unit,
Department of Fisheries and Wildlife Sciences, University of Missouri, Columbia,
Missouri 65211, USA.
*Correspondence author: E-mail: ckwillia@udel.edu

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## Abstract

Population-based habitat conservation planning for migrating and wintering waterfowl in North America is carried out by habitat Joint Venture (JV) initiatives and is based on the premise that food can limit demography (*i.e.* food limitation hypothesis). Consequently, planners use bioenergetic models to estimate food (energy) availability and population-level energy demands at appropriate spatial and temporal scales, and translate these values into regional habitat objectives. While simple in principle, there are both empirical and theoretical challenges associated with calculating energy supply and demand including: 1) estimating food availability, 2) estimating the energy content of specific foods, 3) extrapolating site-specific estimates of food availability to landscapes for focal species, 4) applicability of estimates from a single species to other species, 5) estimating resting metabolic rate, 6) estimating cost of daily behaviours, and 7) estimating costs of thermoregulation or tissue synthesis. Most models being used are daily ration models (DRMs) whose set of simplifying assumptions are well established and whose use is widely accepted and feasible given the empirical data available to populate such models. However, DRMs do not link habitat objectives to metrics of ultimate ecological importance such as individual body condition or survival, and largely only consider food-producing habitats. Agent-based models (ABMs) provide a possible alternative for creating more biologically realistic models under some conditions; however, ABMs require different types of empirical inputs, many of which have yet to be estimated for key North American waterfowl. Decisions about how JVs can best proceed with habitat conservation would benefit from the use of sensitivity analyses that could identify the empirical and theoretical uncertainties that have the greatest influence on efforts to estimate habitat carrying capacity. Development of ABMs at restricted, yet biologically relevant spatial scales, followed by comparisons of their outputs to those generated from more simplistic, deterministic models can provide a means of assessing degrees of dissimilarity in how alternative models describe desired landscape conditions for migrating and wintering waterfowl.

**Key words:** agent-based models, bioenergetics, carrying capacity, daily ration models, energy demand, energy supply, waterfowl.

Population-based, habitat conservation of the North American Waterfowl Management Plan (NAWMP 2012) is planned and implemented by regional, collaborative partnerships named Joint Ventures (JVs). Since 1987, JVs have spent approximately US$5 billion to conserve or manage 7.8 million ha of habitat. Nine JVs set waterfowl habitat objectives and deliver programmes in regions that support the majority of ducks wintering in the United States. Conservation plans developed by these JVs are based on the premise that food during the non-breeding period can limit demographics and thus population trends for waterfowl (*i.e.* the food limitation hypothesis). This hypothesis is supported by research indicating that duck body condition correlates with winter habitat conditions (Delnicki & Reinecke 1986; Lovvorn 1994; Thomas 2004; Heitmeyer 2006; Moon *et al.* 2007), which influences diet quality (Loesch & Kaminski 1989), and moreover that body condition influences survival (*e.g.* Moon & Haukos 2006; Bergan & Smith 1993) and the timing of migration phenology (Heitmeyer 1988, 2006). At the population level, winter habitat conditions can influence the distribution of ducks within and across winters (Nichols *et al.* 1983; Hepp & Hines 1991; Lovvorn & Baldwin 1996; Pearse *et al.* 2012). Finally, there is evidence for cross-seasonal influences, with winter and migration habitat conditions influencing subsequent productivity (Heitmeyer & Fredickson 1981; Kaminski & Gluesing 1987; Raveling & Heitmeyer 1989; Guillemain *et al.* 2008; Devries *et al.* 2008; Anteau & Afton 2009).

Most JVs use a bioenergetics model to estimate habitat carrying capacity and project habitat needs to support waterfowl populations at target levels during the non-breeding season (*e.g.* Prince 1979; Reinecke *et al.* 1989; Petrie *et al.* 2011). Bioenergetics models represent a class of resource depletion models and those used by winter habitat JVs often take the form of daily ration models (DRMs; Goss-Custard *et al.* 2003). While DRMs can take different forms, they generally aggregate food energy density across multiple habitat patches (using either habitat-specific values or average values across habitats) and divide by daily energy demands of a target duck species to estimate the theoretical carrying capacity of a given area (Miller & Newton 1999; Goss-Custard *et al.* 2002; Goss-Custard *et al.* 2003). In its simplest form, carrying capacity may be expressed in terms of duck energy-days (DED):

$$\text{DED} = \frac{\begin{array}{c}\text{Food available}\left(\text{g dry weight}\right)\times\\ \text{True metabolisable energy}\\ \left(\text{kcal/g dry weight}\right)\end{array}}{\begin{array}{c}\text{Daily energy expenditure}\\ \left(\text{kcal/day}\right)\end{array}} \quad (1)$$

Thus, under the assumption that DRMs reasonably reflect foraging dynamics of free-ranging waterfowl, useful calculations of carrying capacity require estimates of: 1) habitat-specific food production (g dry weight per unit area), 2) functional availability of waterfowl foods (g dry weight per unit area; *e.g.* Greer et al. 2009), 3) true metabolisable energy of available foods (kcal per g dry weight; Miller & Reinecke 1984), 4) daily energy requirements of target species (kcal), and 5) region- and species-specific population targets (Petrie *et al.* 2011). The actual forms of models being used by JVs are more sophisticated than the simple equation depicted above. For example, most JVs model energy supply and demand in time and space (*e.g.* Central Valley JV 2006; Pacific Coast JV 2004) with the understanding that energy supplies may be influenced by natural or intentional flooding of habitats and that demand may vary temporally based on population size, migration chronology, changes in species composition, physiological needs, weather and other endogenous or exogenous factors. Regardless of model sophistication, all DRMs require some estimate of energy supply and demand.

While simple in principle, there are

empirical and theoretical challenges associated with estimating energy supply and demand. When estimating energy supply, bias can occur from inaccurate estimates of: 1) food availability, 2) energy content of specific foods, 3) extrapolating site-specific estimates of food availability to landscapes for focal species, or 4) assuming estimates from a single species of waterfowl apply to other species. Likewise, quantitative challenges exist when estimating energy demand during the non-breeding period. Beyond the challenge of estimating regional population size (Soulliere *et al.* 2013), those planning waterfowl management programmes may also face biased estimates of: 1) resting metabolic rate, 2) cost of daily behaviours, and 3) costs of thermoregulation or tissue synthesis. Finally, bioenergetic models can take various forms ranging from simple DRMs to spatially-explicit, agent-based models that incorporate additional mechanistic details of the systems being modelled. However, the conditions dictating when more complicated models are required is not thoroughly understood (Goss-Custard *et al.* 2003).

To address some of these challenges, a special session was convened at the 6th North American Duck Symposium to consider fundamental aspects of the DRMs most commonly used in conservation planning undertaken by winter habitat JVs in North America. A comprehensive assessment and comparison of the strengths, weaknesses and utility of the full suite of conservation planning models for wintering waterfowl were beyond the scope of this paper. Rather, talks addressed several key elements associated with estimating energy supply and demand, along with alternative model structures and the implications of new model advances and pitfalls, for future conservation planning directed towards ducks at staging and wintering sites.

## Energy supply

Calculating energy supply for waterfowl requires an empirical measure of habitat-specific food production and availability to waterfowl. Here we define food availability as the production of food minus an amount not exploitable by waterfowl (*i.e.* the giving-up density, or food availability threshold; Greer *et al.* 2009; Hagy & Kaminski 2012a). When food availability is known or can be reasonably estimated, energy supply can be calculated using energetic values of each food to individual species and extrapolated across the area of interest. Below, we explore each of these components in increased detail.

### Estimating food production

Direct and indirect methods have been developed for estimating food availability in the environment. For dabbling ducks, clipping of inflorescences, extracting soil cores and sweep nets are the primary tools used to estimate the biomass of seeds, nektonic and benthic forage produced (Dugger *et al.* 2008; Kross *et al.* 2008a; Evans-Peters *et al.* 2010; Hagy & Kaminski 2012a).

Vegetative food production is often estimated using floristic measurements (*e.g.* Gray *et al.* 1999a, 2009; Naylor *et al.* 2005) or by assessing seed, tuber and plant part biomass at the end of the growing season (Kross *et al.* 2008a). Seeds can be threshed from inflorescences and collected using core samples (Kross *et al.* 2008a), predicted using vegetation morphology indices (Gray *et al.* 1999a) using visual assessments (Naylor *et al.* 2005), or measured directly using other means (Gray *et al.* 2013). Initially, Laubhan & Fredrickson (1992) developed equations that predicted seed production using phytomorphological measurements. These models were not widely used because they required extensive field measurements and predictions outside of the region of development were unreliable (Gray *et al.* 1999a). Gray *et al.* (2009) determined that the area of a seed head was a reliable predictor of seed mass and developed a simplified process of using desktop scanners to predict seed production. Naylor *et al.* (2005) described a process for ranking moist-soil habitat quality for waterfowl in California, USA, based on visual estimates of plant composition and forage quality. Stafford *et al.* (2011) replicated this technique in Illinois and found that the index explained 65% of the variation in moist-soil plant seed biomass collected from core samples. These rapid assessment techniques allow wetland managers to obtain efficiently general estimates of seed biomass for waterfowl in moist-soil wetlands without extensive and costly laboratory or field work. However, Evans-Peters (2010) suggested these visual assessments omit ≤ 30% of seed biomass in the seed bank. Moreover, accuracy of visual assessments of standing vegetation during the growing season or prior to vegetation senescence and inundation by water may not accurately reflect food densities at later points in time useful to managers (Greer *et al.* 2007; Fleming *et al.* 2012).

Traditional core samplers used for sampling duck foods range from 5–10 cm in diameter (Swanson 1983; Stafford *et al.* 2006; Greer *et al.* 2007; Hagy *et al.* 2012*b*; Smith *et al.* 2012) and 5–10 cm in depth (Greer *et al.* 2007; Kross *et al.* 2008a; Olmstead 2010; Hagy & Kaminski 2012b), with deeper samplers used for larger, longer-necked taxa (*e.g.* 30 cm for swans; Santamaria & Rodriguez-Girones 2002). In relatively shallow water, core samplers may yield simultaneous density estimates for submersed aquatic vegetation (*e.g. Myriophalum* sp., *Ceratophyllum* sp., *Elodia* sp.), nektonic and benthic invertebrates, seeds and tubers (Swanson 1978). In deeper water or in areas with high densities of aquatic vegetation, core samplers may be used in combination with sweep nets (Murkin *et al.* 1996; Tidwell *et al.* 2013), exclusion devices (Straub *et al.* 2012) and box samplers (Synchra & Adamek 2010) to provide better measures of food availability.

Regardless of the direct sampling method used, samples require extensive time to process in the laboratory. Food items typically are sorted from the plant, soil and detritus by hand using a series of graduated sieves, dried to constant mass in a forced air oven, identified and weighed by species or appropriate biological classification. This process is tedious and costly (Stafford *et al.* 2011). Sub-sampling is a well-vetted approach for reducing processing time (*e.g.* Proctor & Marks 1974; Schroth & Kolbe 1993; Murkin *et al.* 1996; Reinecke & Hartke 2005; Smith *et al.* 2012). Waterfowl researchers have recently applied soil core sub-sampling and verified that overall means are similar between sub-sampled and wholeprocessed samples for moist-soil seeds (Hagy *et al.* 2011; Stafford *et al.* 2011), rice *Oryza* sp. grains (Stafford *et al.* 2006) and macroinvertebrates (M. Livolsi *et al.* University of Delaware, unpubl. data), although variance associated with the estimates may increase (Hagy *et al.* 2011).

Currently, there is little information on the optimal sample size for core samples in waterfowl habitats, and some information suggests optimal sample size may be difficult to predict (Reinecke & Hartke 2005; Marty 2013). While current studies often base sample size on financial and temporal constraints (Sherfy *et al.* 2000; Evans-Peters *et al.* 2012), 20–30 samples per patch have been shown to result in coefficient of variation (C.V.) values of < 10% (Dugger *et al.* 2008; Greer *et al.* 2009; Evans-Peters *et al.* 2012). Preliminary power analysis of saltmarsh systems indicates that *c.* 40 samples per habitat type/location/time period would be reasonable for some habitats, but other habitats such as "high-marsh" and rice fields show greater variability and may require significantly more samples (K. Ringelman, University of Delaware, unpubl. data; Marty 2013). More comprehensive research is needed to provide appropriate sample sizes for quantifying food availability within different habitat types.

Food biomass estimates may also be influenced by improper inclusion of prey seldom consumed or not energetically profitable to waterfowl. For example, 30–70% of seeds sorted from core samples collected in the Mississippi Alluvial Valley, USA, in autumn had little nutritional value or were likely not consumed by most dabbling ducks (Hagy & Kaminski 2012b; Olmstead *et al.* 2013). Additionally, biomass estimates may be biased due to incomplete recovery of seeds during sample processing, through non-detection, loss or destruction. Hagy *et al.* (2011) reported that *c.* 14% of known seeds were not recovered from core samples during sorting, and that recovery rates depended on seed size. Thus, energy information based on incomplete recovery could underestimate food availability by 10–20% (Hagy *et al.* 2011), whereas analyses that do not account for actual diet and food use bias could overestimate food availability by as much as 47% (Hagy *et al.* 2011; Olmstead *et al.* 2013).

Finally, biomass estimates may be variable among locations and geographical regions (*e.g.* Stafford *et al.* 2006a; 2011; Kross *et al.* 2008a; Evans-Peters *et al.* 2012; Hagy & Kaminski 2012b); thus, use of local productivity estimates may be biased when scaled to regional levels. A recent simulation of core sampling indicated that detection probabilities for food items varied by food densities, corer size and the underlying pattern of food distribution (A. Behney, Southern Illinois University, unpubl. data). While biologists can use methodological improvements to reduce local variance, they should acknowledge the possibility of geographic variation, random *versus* clumped food distributions within habitats and the possibility that birds may not follow an ideal free distribution or forage optimally. Therefore, biologists may wish to consider sampling in multiple locations to provide a better representation of values for regional-scale habitat management and conservation (*e.g.* Stafford *et al.* 2006; Kross *et al.* 2008a).

## Estimating food availability

Unbiased, precise estimates of food production and its energy density are not sufficient for understanding the energy supply available to migrating and wintering waterfowl, because all foods produced may not be available when waterfowl access habitats, for instance due to the depth or extent (*i.e.* surface area) of flooding (Kross *et al.* 2008b; Foster *et al.* 2010). Assessment of availability includes accounting for physical accessibility and energy acquired given costs of foraging (Hagy *et al.* 2012b).

Use of an area by migrating or wintering waterfowl may lag considerably from the time of seed maturation, and reliance on food production estimates from the end of a growing season may overestimate food available to the birds. Seed abundance in agricultural habitats can decrease substantially between seed maturation and the arrival of waterfowl, especially in mid to southern latitudes of the United States (Manley *et al.* 2004; Stafford *et al.* 2006; Greer *et al.* 2009; Foster *et al.* 2010b). However, Marty (2013) reported an increase in abundance of waste rice in the Gulf Coastal Prairie rice fields of Louisiana and Texas during autumn, due to the production of a second unharvested rice crop (ratoon) in late autumn, following an initial late summer harvest of rice. Seed loss rates vary with hydrology and are attributable to germination, consumption by non-target wildlife and decomposition (Stafford *et al.* 2006; Greer *et al.* 2007; Foster *et al.* 2010a). Hagy *et al.* (2012a) noted that decomposition of moist-soil seeds in flooded emergent wetlands was *c.* 18% per month. Stafford *et al.* (2006) reported that 58% of waste rice in the MAV fields decomposed post-harvest in autumn, compared to 14% and 8% loss from granivory and germination, respectively. Foster *et al.* (2010b) found that monthly rate of loss of seeds for corn *Zea* sp., sorghum *Sorghum* sp. and soybean *Glycine* sp. ranged from 64–84% post-harvest. Decomposition rates likely vary with latitude as warmer temperatures would contribute to higher rates. Thus, production estimates are useful to evaluate management actions, but sampling should either be timed to coincide with waterfowl arrival or appropriate adjustments are needed to initial estimates, to account for seed loss not attributable to waterfowl foraging.

The physical availability of foods for waterfowl depends on the birds' ability to extract foods from wetlands (*e.g.* Nolet *et al.* 2001). Studies of seed and invertebrate biomass have traditionally assumed that every seed or invertebrate captured in the 5–10 cm deep core samples was available to foraging waterfowl. However, species with different foraging behaviours and morphologies (*e.g.* diving ducks *Aytha* sp. *versus* dabbling ducks *Anas* sp.) can affect how much of the production is actually available (Nudds & Kaminski 1984; Murkin *et al.* 1996; Sherfy *et al.* 2000; Evans-Peters 2010; Olmstead 2010). Additionally, foraging efficiency varies with sediment depths and seed type, and it is likely that seeds buried at greater depths may be less profitable energetically (Nolet *et al.* 2001; Smith *et al.* 2011). However, if biologists sample systems with large amounts of macroinvertebrates moving within the soil column, especially in a tidal system, deeper sampling depths may be more appropriate to estimate food availability (although this has yet to be tested).

From behavioural and energetic perspectives, estimates of food availability must be adjusted when food densities are too low for energetically profitable foraging (van Gils *et al.* 2004; Nolet *et al.* 2006; Hagy *et al.* 2012b). There is evidence for a critical food density that remains after individuals either give up foraging (Greer *et al.* 2009) or no longer remove food from patches despite continued foraging effort (Hagy 2010; Hagy *et al.* 2012b). However, the critical food density varies among habitats, regions and potentially even between foraging patches that differ in food composition (Baldassarre & Bolen 1984; Naylor 2002; Greer *et al.* 2009; Hagy 2010). For example, Hagy (2010) noted that foraging thresholds varied widely for moist-soil wetlands, but they were likely at least 200 kg/ha in natural moist-soil wetlands with a wide variety of seed taxa present. Hagy et al (2012b) reported residual seed densities exceeding 250kg/ha in moist-soil wetlands in the MAV after waterfowl ceased to remove additional foods, whereas Naylor (2002) reported residual densities of 30–160 kg/ha in these wetlands in California. Greer *et al.* (2009) and Baldassarre & Bolen (1984) reported residual densities of 50 kg/ha or less in flooded rice and dry corn fields, respectively. Gray *et al.* (2013) provided updated estimates of available food for waterfowl in agricultural fields, moist-soil wetlands and bottomland hardwoods, and incorporated critical food densities into these estimates. Application of fixed critical food densities probably results in inaccurate predictions at the patch level (van Gils *et al.* 2004), but are compatible with daily ration models currently used to predict carrying capacity for large regions (*e.g.* Soulliere *et al.* 2007) and may have some value if patch-specific data are unavailable or impractical to obtain. Therefore, incorporating critical food densities at the patch level will likely increase the accuracy of food availability estimates. Ancillary modelling has indicated that failure to apply foraging thresholds accurately at the patch level could affect food availability estimates by as much as 60%, and this bias varies with values of foraging thresholds and seed density (Pearse & Stafford 2014; H. Hagy, Mississippi State University, unpubl. data).

## True metabolisable energy of foods

True metabolisable energy (TME, kcal/g) represents the amount of energy an individual bird receives from a food item, after accounting for metabolic faecal losses and also endogenous urinary losses as metabolised energy (Miller & Reinecke 1984). The TME provides a more accurate estimate of metabolised energy than apparent metabolisable energy (AME), because TME accounts for faecal and urinary losses (Miller & Reinecke 1984; Karasov 1990). The TME of waterfowl foods are important components for accurate assessments of waterfowl bioenergetics and energetic carrying capacity. It may be calculated: a) indirectly, using a regression model of total excretory energy on total food intake, or b) experimentally, determined by feeding birds a controlled diet and measuring excretory energy (Sibbald 1975; Sibbald 1979;

Kaminski & Essig 1992). The TME values can then be used to calculate available energy by multiplying the mass of a food item by its TME value and extrapolating the resulting energy value across an area of interest.

Nonetheless, there is a lack of TME values for common waterfowl foods and species. Current studies have focused on TME values for Mallard *Anas platyrynchos*, American Black Duck *A. rubripes*, Northern Pintail *A. acuta*, Canada Goose *Branta canadensis*, Blue-winged Teal *A. discors* and Carolina Wood Duck *Aix sponsa* (Hoffman & Bookhout 1985; Jorde & Owne 1988; Petrie 1994; Reinecke *et al.* 1989; Petrie *et al.* 1998; Sherfy 1999; Sherfy *et al.* 2001; Checkett *et al.* 2002; Kaminski *et al.* 2003; Ballard *et al.* 2004; Dugger *et al.* 2007; J. Coluccy *et al.*, Ducks Unlimited, unpubl. data). There is uncertainty associated with applying a TME value to a species other than the one from which it was derived. However, closely related bird species will likely have similar TME values for a given food item due to similarities in gut morphology. While this hypothesis needs to be tested, substituting TME values among similar bird species may suffice when evaluating energy content of food items until species-specific TME values become available.

Another problem with the lack of information on TME values is that existing studies have typically determined TME values for only a few seed or invertebrate species across a select few families. Therefore, researchers are forced to "fill in the gaps" by assigning TME values based on educated guesses with information from few studies. For example, many JVs use a mean seed TME value of 2.5 kcals/g for their projections of moist-soil seeds; however, data from the Lower Klamath National Wildlife Refuge, in northern California, indicate that mean seed TME values can be less than 50% of this estimate (Dugger *et al.* 2008). Most existing TME data are for seed species from the Midwestern United States, and employing TME averages may therefore be inappropriate in regions where seed composition is significantly different. Calculating potential available energy across large areas using variable or biased TME values may result in meaningless estimates of carrying capacity. Thus, additional research efforts focused on deriving TME values experimentally for a wide variety of common food items for waterfowl species will increase precision and accuracy of energetic carrying capacity estimates. Alternatively, because such comprehensive analyses may be impractical, future tests that extrapolate partial knowledge may be of use. For example, researchers could derive TME values for a single plant seed species for a range of duck species that differ in body size and diet (Green-winged Teal *A. crecca*, American Wigeon *A. americana*, Northern Shoveler *A. clypeata*, Mallard) to yield insight into the extrapolation and applicability of TME values for species that have not been included in TME experiments. Alternatively, researchers could relate TME to nutritional composition of the seeds because digestibility of multi-species forage is related to the amount of indigestible fibre. Additionally, researchers may evaluate if known TME values of common waterfowl foods can be predicted from gross energy (GE) estimates of these foods (*e.g.*

Kaminski *et al.* 2003). If GE would explain significant variation in TME (*e.g.* ≥ 70%) such models may be used cost-effectively for habitat conservation planning and implementation.

## Extrapolating energy supply to the landscape

Because of the significant potential for biological and sampling error discussed above, the notion of extrapolating estimated useable energy to a landscape level should be approached with caution. Inherently, the potential for multiplication of errors may cause landscape-level variance to be too large to make meaningful management recommendations. However, an equally difficult problem is to quantify correctly what habitat is actually available to waterfowl species.

Various geospatial data have been used to quantify characteristics of important waterfowl habitats (*e.g.* the National Wetlands Inventory (NWI) and National Land Cover Data). However, there are inherent limitations associated with the accuracy of these data. For example, the NWI established by the U.S. Fish and Wildlife Service to conduct a nationwide inventory of wetlands by type is widely used for quantifying the availability of wetlands on staging and wintering areas. Unfortunately, the NWI does not capture and classify all wetlands accurately because NWI maps are derived from aerial photo-interpretation with varying limitations due to scale, photograph quality, inventory techniques and other factors (Federal Geographic Data Committee 2008; Dahl *et al.* 2009). Recent advances in GIS technology, the availability of higher resolution imagery, the integration of NWI data with other geospatial data sources (*e.g.* LiDAR, soil maps, *etc.*) and the development of standardised techniques for wetland identification and delineation have substantially improved the NWI (Dahl *et al.* 2009; Knight *et al.* 2013). However, NWI data are currently only available for 89% of continental United States, and the average date of the NWI for most of the U.S. is from the 1980s. Currently, NWI data are being updated at a rate of ≤ 2% per year due to funding reductions (J. Coluccy, Ducks Unlimited, pers. comm.). Similar limitations exist for quantifying non-wetland habitat types (*e.g.* county crop data or seasonally-flooded cropland). These limitations have hampered efforts to estimate habitat availability accurately for wintering waterfowl, especially at frequencies desired for maintaining a contemporary understanding of the landscape carrying capacity.

In addition to error associated with estimating wetland habitats correctly, biologists need to consider potential indirect impacts of human developments and disturbance that make available habitat avoided and thus reduce carrying capacity (Korschgen & Dahlgren 1992; St. James *et al.* 2013). Often, estimates of available habitat are quickly calculated with the assumption that all wetlands are created equal and waterfowl have unimpeded access to them. However, avoidance behaviour may occur at various temporal and spatial scales, ranging between not settling in an area and/or not utilising a space to its maximum potential (Korschgen & Dahlgren 1992; Laundré *et al.* 2010; Hine *et al.* 2013). While some waterfowl species such as Canada Geese and Mallard may have adapted well to an altered landscape, other species of special concern appear to be particularly sensitive to disturbance (Korschgren & Dahlgren 1992) including Atlantic Brant *Branta bernicla*, American Black Ducks, Canvasback *Aythya valisineria* and Lesser Scaup *Aythya affinis*. Additionally, ducks with a smaller body size and shorter longevity (*e.g.* Green-winged Teal) than larger species (*e.g.* Mallard) may take more risks to forage or otherwise use wetlands that are hunted, and thus exhibit reduced avoidance behaviour (St. James 2011).

For planning purposes, it is important for resource managers to understand how waterfowl separate themselves from anthropogenic development and respond to disturbance, and how these factors influence their ability to extract critical food resources from habitats. For example, on Lake St. Clair between Michigan and Ontario, autumn-staging diving ducks shifted their use of traditional feeding and loafing areas on the U.S. side of the lake to new areas on the Canadian side (Shirkey 2012). Warmer weather and associated increased angling and hunting activity on the U.S. side throughout autumn and early winter is considered to have resulted in a significant shift in habitats important to Canvasback and Lesser Scaup (Shirkey 2012). Diving ducks had options at this location, but obviously disturbance is an important management consideration at staging sites.

## Energy demand

In addition to knowing energy availability in the landscape, calculating habitat carrying capacity requires an estimation of the energy needs of individual waterfowl on any given location and day. Energy requirements of a wild vertebrate (or Daily Energy Expenditure, DEE) are usually estimated as the sum of the energy costs of maintenance (or Resting Metabolic Rate, RMR), activity and thermoregulation (King 1973; Servello *et al.* 2005; Fig. 1). If the animal is growing or reproducing, then an additional energy cost associated with this production must be added (Fig. 1). If the animal is not in a steady state and storing energy, then this cost also must be added to the daily energy costs for the animal (Fig. 1). Most bioenergetics approaches currently used by JVs for estimating DEE of waterfowl do not account for the energy costs of thermoregulation, production and storage, thereby reducing DEE to an estimate of energy expenditure through daily activities (Fig. 1). We will summarise current views on estimating resting metabolic rate, the energetic costs of daily activity and the costs of thermoregulation.

### Resting metabolic rate

The RMR is usually defined as energy costs of maintaining an animal's physiological systems under a certain, restricted set of conditions including: 1) no activity, 2) no cost of staying warm or cool when measured at ambient temperatures that are within the thermoneutral zone of the animal, 3) no growth or reproduction, and 4) the bird is at steady state and not accumulating any fat or protein reserves or depleting them. Because of these restrictive conditions, there have been few replicated RMR studies for duck species. However,

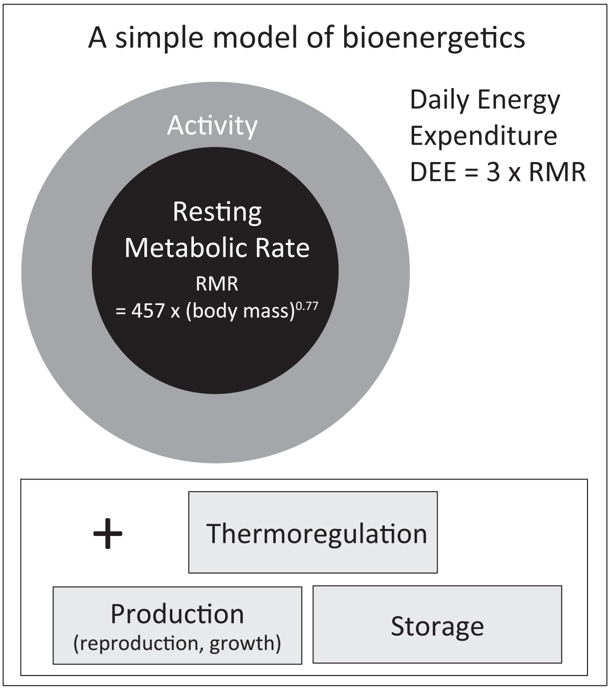

**Figure 1.** A conceptual bioenergetics model of the key components that comprise Daily Energy Expenditure (DEE) of a wild vertebrate. DEE is usually estimated as the sum of the energy costs of maintenance (or Resting Metabolic Rate, RMR, calculated from body mass; Miller & Eadie 2006), times 3 to account for activity. Most bioenergetics approaches do not account for the energy costs of thermoregulation, production and storage, thereby reducing DEE to an estimate of energy expenditure through daily activities.

there is established literature on the allometric scaling of RMR of a wide variety of animals (Kleiber 1932, 1961; Prince 1979; Schmidt-Nielsen 1984; Peters 1983; Calder 1984; Brown & West 2000) following:

$$\mathrm{RMR} = a(\mathrm{Mass})^b \qquad (2)$$

where $a$ = a mass proportionality coefficient, Mass = body mass (kg), and $b$ = slope of the regression line on a log scale. In general, the accuracy of RMR predictions from body size improves substantially when subsets of species such as waterfowl are considered. Miller & Eadie (2006) used all available data from waterfowl RMR to update estimates of the slope ($b$) and intercept ($a$) parameters for waterfowl. For JV carrying capacity modelling, this provides a relatively straightforward method to estimate RMR for this component of bioenergetics modelling (but see caveats in Miller & Eadie 2006).

### Activity expenditures

Daily Energy Expenditure is based on the previously estimated RMR times the cost of activity. Most bioenergetics models used by JVs calculate DEE as

$$\text{DEE} = \text{RMR} \times 3 \tag{3}$$

with the multiplier "3" accounting for the average amount of energy expended on activity in any given day (King 1974; Prince 1979; Miller & Eadie 2006). However, if ducks are storing energy, then this adds further energy costs (*e.g.* Heitmeyer 2006 used a 3.4 multiplier for Mallard in winter). While this methodology provides an estimate of DEE, there are questions as to whether this simple approach accurately accounts for variability in behaviour due to external variations (*e.g.* temperature, tide, time of day, month, latitude, harvest pressure, disturbance, *etc.*) that are known to influence both daily activities and DEE (Weathers 1979; Albright *et al.* 1983; Brodsky & Weatherhead 1985; Morton *et al.* 1989). Miller & Eadie (2006) demonstrated that estimates of carrying capacity were highly sensitive to the multiple of RMR used, as well as the mass proportionality coefficient (*a*) from the allometric equation. Thus, the use of a single multiplier for adjusting RMR is likely an oversimplification. Depending on the sophistication of the planning process, JVs could use more refined estimates of activity costs derived from measured time-activity budgets of waterfowl in a given area for which DEE is to be estimated (see Weathers *et al.* 1984; Miller & Eadie 2006). Time-activity budgets rely on extensive behavioural observations to determine a time budget or the percentage of time free-living individuals spend in different behavioural states. Using behaviour-specific factorial increases in energy expenditure over RMR, a time budget can be converted into estimates of energy expenditure or an energy budget (Albright *et al.* 1983; Paulus 1988). Therefore, equation (3) can be expanded to account for multiple activities:

$$\text{DEE} = \sum_{i=1}^{n}\left[(\text{RMR} \times a_i) \times T_i\right] \tag{4}$$

where $a_i$ = the activity-specific factorial increase in RMR for the *i*th behavioural activity and $T_i$ = the proportion of time engaged in the activity within the 24-hr cycle. For example, Wooley (1976) added heart rate monitors to five Black Ducks and estimated multiplier values of 1.7 for feeding, 1.2 for resting, 2.1 for comfort, 2.2 for swimming, 2.2 for alert, 12.5 for flying, 1.7 for walking, 2.4 for agonistic and 2.4 for courtship. Finally, the activity-specific factorial increase in RMR, $a_i$, was estimated by Wooley (1976). However, due to the crude nature of this study as compared to a more controlled respirometry study, the validity of the estimates has been queried. For example, how could comfort behaviour be energetically more taxing than feeding? If these estimates are biased, the implications for scaling up to the population level duck-use days could be flawed. Additional studies that measure BMR accurately for many waterfowl species (see McKechnie & Wolf 2004), and consider how environmental factors including cold ambient temperatures affect BMR and DEE (*e.g.* McKechnie 2008; McKinney & McWilliams 2005), can provide more precise estimates of DEE for waterfowl.

Estimating DEE through time-energy budgets is labour intensive, time consuming, assumes random observability, does not account for energetically taxing flight behaviour and is historically limited to diurnal observations (Jorde & Owen 1988). Recently, Jones (2012) conducted a comprehensive analysis of different measures of daily activity energy expenditures using American Black Ducks in coastal New Jersey. Black Duck behaviour (including flying) was quantified during morning crepuscular, diurnal, evening crepuscular and nocturnal periods to create a 24-hr time-energy budget. Behaviours and energy expenditure differed between periods and months, with greatest hourly energy expenditure during the morning crepuscular period and lowest during the nocturnal period. Additionally, precipitation, temperature and tide influenced variation in Black Duck behaviours over the 24-hr period. Moreover, anthropogenic disturbance factors influenced behaviour including increased feeding during diurnal and nocturnal periods on areas open to hunting when the hunting season was closed, and increased resting on areas closed to hunting regardless of whether the hunting season was open. As a result of the detailed time energy budget, DEE was estimated as being 1,218 ± s.e. 19.36 kJ/bird/day, or 2.4 times RMR. The same estimate calculated using RMR times 3 was 21% greater at 1,545 kJ/bird/day, or 21% higher. If one were to apply both estimates to 101,017 ha of New Jersey coastal habitat for which energy supplies were estimated (Cramer *et al.* 2012), autumn carrying capacity would be ~55,000 ducks while the 24-hr time energy budget estimates would predict a carrying capacity of ~70,000 ducks, closer to the estimated 75,000 Black Ducks estimated by mid-winter surveys (USFWS MBDC 2014).

## Cost of thermoregulation

The assumption that waterfowl are not incurring energy costs of thermoregulation, production and storage requires some scrutiny. Waterfowl and all endotherms must increase energy expenditure when ambient temperature is below the lower critical temperature (LCT) or above the upper critical temperature (UCT) of the animal (Fig. 2):

$$m_c * \Delta T_{\mathrm{LCT}\text{-}Ta} \qquad (5)$$

where $m_c$ is the slope of increasing metabolic energy above the lowest critical temperature (LCT) and $\Delta T_{\mathrm{LCT}\text{-}Ta}$ is the difference in ambient temperature from the lowest critical temperature. This allows for an expansion of equation (4):

$$\mathrm{DEE} = \sum_{i=1}^{n} \left[ \left( (\mathrm{RMR} \times a_i) + CT \right) \times T_i \right] \qquad (6)$$

where $CT$ = the cost of thermoregulation at a specified temperature (kJ/bird/h) in addition to activity-specific increases to RMR. The UCT is rarely considered, as most temperate waterfowl avoid regions with temperatures above the UCT. However, waterfowl during winter may often encounter periods when the ambient temperature is below their LCT. For example, the LCT of brant is 7.5°C (Morehouse 1974); below this ambient temperature, brant would expend additional energy to stay warm. Generally, because thermal conductivity of water is 23 times greater than that of air, waterfowl sitting on

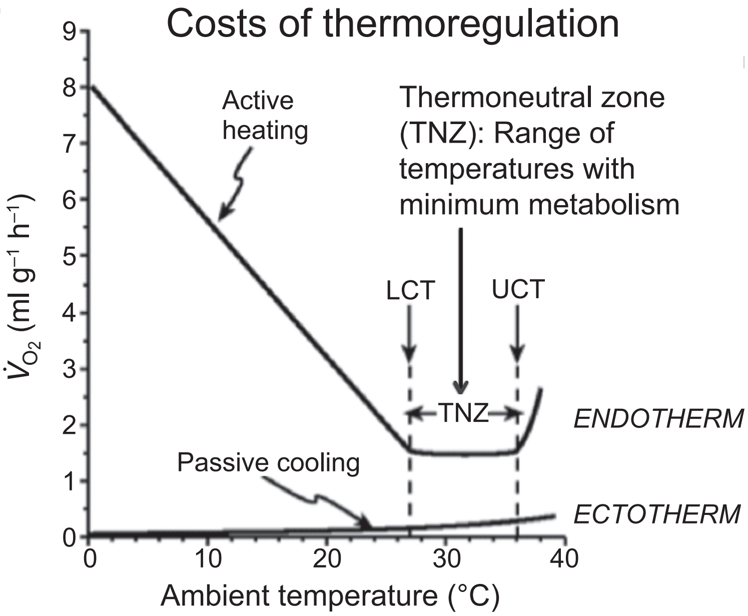

**Figure 2.** Any endothermic animal incurs additional energy costs when ambient temperatures drop below their lower critical temperature (LCT). These additional costs are linearly related to ambient temperatures below the LCT and are directly a function of the insulative properties of the animal. From Hiebert & Noveral (2007).

water would need to expend much more energy to stay warm compared to birds sitting on shore at the same ambient air temperature. While Richman & Lovvorn (2011) did not find noticeable differences in energy costs for Common Eiders *Somateria mollissima*, in cold water or air, McKinney & McWilliams (2005) estimated that the energy costs of thermoregulation in water could contribute as much as 13–23% of DEE for Bufflehead *Bucephala albeola* during winter in southern New England. Therefore, if DEE is estimated for waterfowl during winter when temperatures are typically below the LCT, including the explicit energy cost of thermoregulation will reduce bias in DEE estimates. However, there is a need for empirical studies of the energy costs of thermoregulation in other waterfowl species to provide a strong foundation for such estimates.

## Alternative modelling frameworks

While addressing sources of variation associated with energy supply and demand is fundamental to reliable bioenergetics models, there is also value in considering if alternative modelling frameworks could improve conservation planning for wintering waterfowl. The DRMs have provided a useful approach for estimating bioenergetic needs and landscape carrying capacity for waterfowl in winter for most non-breeding JVs in North America for several reasons: 1) they are well-established and widely accepted, 2) they provide a tool for translating waterfowl population objectives into habitat-based objectives, which is essential to accomplish NAWMP continental goals, 3) they are based on data that can be obtained and validated from field surveys/ research (*e.g.* food abundance and daily energy demand), and 4) they allow managers and planners to evaluate the effect of large-scale habitat changes on the availability of food resources and so provide an ability to undertake scenario planning (Central Valley JV Implementation Plan 2006).

However, there are a number of limitations of the DRMs. The DRMs are not spatially explicit, because they assume no cost of travelling between food patches, and food availability is considered to be relatively uniform across the landscape. The set of simplifying assumptions incorporated into most DRMs (*e.g.* ideal free foragers) precludes consideration of how habitat heterogeneity or bird distribution patterns (spatially or temporally) influence carrying capacity. Likewise, in DRM, energy demand is summed over all individuals regardless of sex and age, usually over extended time periods (bi-weekly), and with DEEs that are assumed to be invariant over time (fixed energy costs). In some cases, JVs will sum DEE across all species based on an average or representative body size.

Changes in energy expenditures throughout the non-breeding season, due to changing food availability, temporal differences in thermoregulatory and individual state-strategies (*e.g.* the need to acquire energy reserves in preparation for migration), and interaction with other fitness-maximising strategies (*e.g.* risk aversion, courtship and mate defence), generally are not included in DRMs. A further limitation of current DRMs is that they consider only energy and not other nutrient resource needs from foraging habitat. Yet other habitats, such as roosting or refuge sites with better thermal characteristics, reduced disturbance or fewer predators, may also be important for reliable conservation planning. Finally, the suite of response variables in DRMs is limited, resulting in a conglomerate energy supply and summed population energy demand that yields a surplus or deficit determined on the habitat base available.

One of the challenges for JVs concerned with science-based habitat conservation for non-breeding waterfowl is to develop a measure of how achieving habitat objectives ultimately affects waterfowl demographic parameters. Current DRMs do not make this link, which limits the ability of habitat managers to integrate planning models with demographic models that predict effects of regional actions on waterfowl dynamics at the continental scale. An alternative approach to DRMs is use of agent-based models (hereafter referred to as ABMs). Unlike the top-down population-based approach of DRMs (summed energy demand and supply functions across species and habitats), ABMs instead represent a "bottom-up" approach where systems are modelled as collections of unique individuals or "agents". Unlike more formal mathematical population models, in ABMs the system dynamics emerge from interactions of individuals and their environment. Models are solved by simulation instead of analytical solutions. Given plausible and realistic "rules" of interaction and behaviour, the outcome is determined by simulation of how the agents in the model respond according to the rules and parameters defined.

The ABMs are now beginning to see broad application in conservation fields, although they have been used in ecological research for well over two decades (DeAngelis & Gross 1992; Sutherland & Allport 1994; Goss-Custard *et al.* 2003; Grimm & Railsback 2005; Stillman 2008). McLane *et al.* (2011) recently provided a comprehensive review of use and utility of ABMs in wildlife ecology and management. Several ABMs have been developed that could provide a platform for modification and use by the NAWMP community to model and plan for waterfowl and waterbird use of managed wetlands. Stillman's MORPH programme (Stillman 2008; West *et al.* 2011) provides a foraging model that has been applied to coastal birds in estuarine environments and has broad potential as a platform for extension to other waterbirds and waterfowl. Pettifor *et al.* (2000) developed a spatially explicit, individual-based, behavioural model to examine the annual cycle of migratory geese. Mathevet *et al.* (2003) developed an ABM model as a management tool for waterfowl conservation incorporating farming and hunting practices in France. However, they did not model duck energetics explicitly and instead relied on a spatially-located DRM. Most recently, the Eadie & Shank research group at UC Davis developed a prototype ABM referred to as SWAMP (Spatially-explicit Waterbird Agent-based Modeling Program) to model overwintering waterfowl bioenergetics (Miller *et al.* 2014; K. Ringelman *et al.*, unpubl. data; J. Eadie *et al.*, unpubl. data). This model is intended to provide similar functionality as DRMs, although it is one of the few ABMs specifically designed for use in landscape-based conservation management. The first prototype has been tested, validated and peer-reviewed (Miller *et al.* 2014).

## What are the advantages of an agent-based approach?

Why might we need a potentially more complex approach to plan for habitat needs of migrating and wintering waterfowl? Conceptually and pragmatically, exploring and developing an ABM approach includes nine potential advantages. First, ABMs link the behaviour of individuals with population- or community-level processes – "scaling upwards". This provides an opportunity to incorporate individual variation among birds and different populations in different locations or over time. It reveals local effects that could have larger scale impacts (local sinks) that might allow planners to target conservation efforts more effectively. Second, ABMs provide the ability to model individual and population performance metrics of ultimate interest to JVs, such as body condition and survival. Thus, an ABM approach may enable functional integration of habitat changes on wintering and staging areas with regional and continental demographic impacts. Third, ABMs provide a more mechanistic structure for foraging behaviour and dynamics that allows for inclusion of more biologically realistic behaviour (*e.g.* foraging rules, patch choice criteria, flocking, *etc.*) than a generic DRM that subsumes and potentially confounds a large amount of important biology. Fourth, ABMs permit spatially explicit analysis of the effects of alternative management regimes on the area and geographic distribution of wetland habitats. Fifth, ABMs provide a useful tool for cross-boundary JV planning. The condition of birds in one JV region might influence their decision about when to migrate to another region, and the condition of birds when they arrive in a JV region might influence how long they stay. The ABMs provide a method by which to track and link body condition and movement of birds across larger spatial scales. Sixth, the ABMs allow planners to model large numbers (millions) of birds in real time, and on large and small spatial scales, using GIS layers as input. Seventh, ABMs can incorporate other important determinants of habitat use and carrying capacity such as disturbance and dispersion of non-foraging (refuge) habitat. Eighth, ABMs offer the potential to expand the capacity to generalise across taxa, including waterfowl, shorebirds and other wetland-dependent wildlife. Ninth, we can use these models to integrate more directly and completely with existing models of water management, in-stream fish habitat, urban growth, and other spatially-based conservation issues (J. Fleskes, U.S. Geological Survey, pers. comm.).

## Challenges of an agent-based approach

Agent-based models are not a panacea for conservation planning. While they offer advantages and potential new insights, we have identified at least three challenges of implementing an ABM approach. First, the richness of possible combinations of deterministic and stochastic processes can make it daunting to simulate through a sufficient range of scenarios to be confident of generating results with a high level of repeatability and generality. Sensitivity analyses are essential, and careful thought and description (and some simplification) are necessary, especially in the early development of a model. Second, ABMs can be complex with a large number of parameters and functions to be estimated. This complexity deterred progress with ABM, because models were specific to a particular situation, not transparent, and not easily communicated or vetted by the scientific and management communities (Grimm & Railsback 2005). However, the field has become sufficiently advanced and well-defined protocols have been established (*e.g.* Grimm *et al.* 2006, 2010). Yet, many parameters are unknown or based on expert opinion. The ABMs are not alone in this regard; traditional DRMs also include a large number of variables and can be extremely complex (*e.g.* the TRUEMET bioenergetic modelling application includes up to 77 time-dependent and 41 time-independent variables). Lastly, ABMs, like DRMs, require a strong foundation of empirical data upon which to base the model and validation. Hence, the sampling and calculation challenges discussed above for DRMs also apply to ABMs. The ABMs allow for heterogeneity in many of these parameters (*e.g.* DEE as a function of daily mass). Although integrating heterogenity is more realistic, it can also generate increased variation in predicted outcomes. As with any modelling exercise, the quality of output is dictated by the quality and validity of the parameters and functions used as input. Field and laboratory research to refine parameters, estimate unknown parameters and validate outputs are essential.

Given these challenges, do we really need more complex models? Goss-Custard *et al.* (2003) tested carrying capacity predictions between a DRM and a spatial depletion model (SDM) and concluded that predictions were similar under certain circumstances. Comparisons of the output from SWAMP with TRUEMET corroborate this similarity (K. Ringelman *et al.*, unpubl. data). Hence, DRMs may be sufficient for basic determination of foraging habitat needs, with the caveat that DRMs may not reflect energy balance perfectly and uncertainty may be high.

So, when do we need spatially explicit behaviour-based models? We envision several conditions when an ABM approach would be valuable, when: 1) time and energy costs of foraging differ between patches, 2) cost of movement between patches is great and varies over time (*e.g.* with patch depletion close to refuges), 3) sequence of use of patches varies but is important, 4) distance from roosting sites or refuges to foraging patches varies and changes over time, 5) juxtaposition and location of habitats are important, 6) non-foraging habitat is important and managers need to assess consequences and interactions of disturbance, sanctuary, predation and public access, among other non-foraging needs, and 7) there is a need to link habitat conditions to key individual (*e.g.* body condition) and population performance (*e.g.* survival) metrics.

Admittedly, there is a trade-off between complexity and utility, and we need to be vigilant against creating increasingly complex models simply because it is possible. However, the ability to address uncertainty in a more formal and explicit manner, the value of a mechanistic approach that potentially can link habitat to demography, and the ability to consider smaller-scale spatially-explicit planning for waterfowl conservation (*e.g.* by providing non-foraging habitat and refuge areas), provide a strong argument to continue developing and learning from ABM approaches.

## Future research and management considerations

Research has made substantial advances to address empirical uncertainties and test assumptions of JV biological planning models over the past several decades. Such research has greatly increased our confidence in the utility of DRMs as a conservation planning tool under certain applications. However, it has also revealed a need to embrace more formal means of identifying model components and parameters and refining them, while also considering alternative modelling frameworks that may produce more reliable conservation planning strategies. Perturbation Analyses or Structural Decision Making are useful tools for considering such uncertainty (Caswell 2001; Hoekman *et al.* 2002, 2006; Coluccy *et al.* 2008), and managers planning the conservation of wintering waterfowl may want to consider expanding their use of such tools.

During our special session and this review, we identified a subset of key simplifying assumptions common to DRMs, some of which deserve additional scrutiny and refinement (*e.g.* constant BMR multipliers). With few exceptions, potential implications of these assumptions and model uncertainties for habitat conservation objectives and priorities have not been quantified (*cf.* Miller & Eadie 2006). Variability, whether originating from natural processes or sampling strategies, is an integral part of any biological system being modelled (*e.g.* Saether *et al.* 2008), yet most DRMs currently being used are deterministic. Even in the few cases where quantitative analyses of variability have occurred, the results have not yet been widely incorporated into conservation recommendations or used to prioritise future investment in science. Thus, a fundamental question is whether habitat objectives arrived at using models based solely on measures of central tendency (*e.g.* mean population abundance, mean TME values) can produce landscapes necessary to achieve NAWMP goals (Straub *et al.* 2012).

Recent progress in our understanding of waterfowl foraging ecology and the successful application of ABMs to inform habitat conservation for coastal waterbirds (*e.g.* Stillman & Goss-Custard 2010) are compelling JV conservation planners to consider the development and use of alternative frameworks for establishing habitat objectives. However, ABMs may be accompanied by even greater uncertainties and requirements for scientific investigations to parameterise, evaluate and refine them. Thus, deliberate considerations must be made to determine if the advantages of more complex models outweigh their greater financial and logistical costs. An initial approach could include developing an ABM at a restricted yet biologically relevant spatial scale, followed by a comparison of their outputs to those generated from more simplistic, deterministic models as a means of assessing degrees of dissimilarity in how alternative models describe desired landscape conditions. Logically, sophisticated models with outputs only marginally different from simpler models would likely not be worthy of adoption (*e.g.* Goss-Custard *et al.* 2003). Moreover, because conservation plans are implemented by the broader JV community, understanding of key models and model-based conservation recommendations is essential for maximum partner engagement and support.

Finally, the challenges associated with developing and refining better biological models are likely to increase as JVs explore strategies to achieve the integrated goals of the current version of NAWMP (NAWMP 2012), which will likely require investments in human dimensions that have until now been at the periphery of JV activities. Skillful evaluation of the costs and benefits to include financial, ecological and evaluation of alternative carrying capacity models and additional model refinements should invoke prudent decisions about their necessity. Just as the waterfowl management community has applied rigorous science to ensure efficient and effective expenditure of limited conservation dollars, so too should it be the foundation for expenditure of science resources, which are often far more limited.

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