Error propagation in energetic carrying capacity models

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ABSTRACT: Conservation objectives derived from carrying capacity models have been used to inform management of landscapes for wildlife populations. Energetic carrying capacity models are particularly useful in conservation planning for wildlife; these models use estimates of food abundance and energetic requirements of wildlife to target conservation actions. We provide a general method for incorporating a foraging threshold (i.e., density of food at which foraging becomes unprofitable) when estimating food availability with energetic carrying capacity models. We use a hypothetical example to describe how past methods for adjustment of foraging thresholds biased results of energetic carrying capacity models in certain instances. Adjusting foraging thresholds at the patch level of the species of interest provides results consistent with ecological foraging theory. Presentation of two case studies suggest variation in bias which, in certain instances, created large errors in conservation objectives and may have led to inefficient allocation of limited resources. Our results also illustrate how small errors or biases in application of input parameters, when extrapolated to large spatial extents, propagate errors in conservation planning and can have negative implications for target populations.

INTRODUCTION

Carrying capacity, the maximum number of organisms that a given area can support during a given time without environmental or resource degradation, is a core concept in wildlife ecology that has direct implications for management and landscape-scale conservation planning. Knowledge of carrying capacity is required to estimate the amount and type of habitats needed to sustain healthy wildlife populations. Inherent in any characterization of carrying capacity is that specific resources are limiting, such as areas for rearing young (e.g., nest sites), cover, or food.

In regions where adequate food resources may limit wildlife populations, estimates of carrying capacity can be derived from estimates of food available to resident and migratory populations. Food-based carrying capacity may be referred to by a variety of terms. For example, studies of ungulates have estimated nutritional carrying capacity (e.g., Wallmo et al. 1977, Hobbs et al. 1982, Beck et al. 2006), whereas avian studies often use the term energetic carrying capacity (ECC; e.g., Haukos and Smith 1993, Anderson and Smith 1999, Guthery 1999, Brasher et al. 2007). Regardless, most approaches to estimate carrying capacity use daily ration models, whereby estimated abundance of food is compared with overall energy requirements of individuals within a defined area (e.g., Heitmeyer 1989, Reinecke and Loesch 1996, Goss-Custard et al. 2003). Some daily ration models consider aspects of foraging theory in calculations of food density (Stephens and Krebs 1986) by incorporating a foraging threshold or critical food density to account for food that animals are unable to profitably extract from the environment (Brown 1988).

Carrying capacity models have been used to inform conservation planning in numerous areas and for various species (e.g., DeYoung et al. 2000, Wilson and Esslinger 2002, Central Valley Joint Venture 2006, Soulliere et al. 2007). These models can be valuable for strategic conservation planning, especially models that integrate foraging theory and other ecological concepts to provide results more reflective of reality (e.g., van Gils et al. 2004, Beck et al. 2006, Windels and Hewitt 2011). Conservation planners use ECC models to quantify how much and what types of foraging habitats are sufficient to sustain an expected number of animals over some specified time period. Output from ECC models express animal abundances and energetic needs into scientifically defensible habitat area goals for a region of interest, which can be stepped down to specific locations (e.g., wildlife refuge) and to specific partners (e.g., state game agencies).

Herein, we present an explicit method for adjustment of food-density estimates with a foraging threshold in the context of daily ration models. The impetus for explicitly describing this adjustment was based on inspection of ECC models currently used for conservation planning and management of non-breeding waterfowl in North America. Generally we found that adjusting food density with a foraging threshold may be more involved than previously described and implemented in conservation planning models currently in use (e.g., Reinecke and Loesch 1996, Wilson and Esslinger 2002, Central Valley Joint Venture 2006). We use hypothetical and real datasets to demonstrate how past colloquial implementations of foraging thresholds may have led to biased estimates of food availability. Moreover, this finding illustrates how seemingly trivial errors can influence landscape-scale conservation planning efforts profoundly. Finally, we illustrate how bias in these estimates can influence output from ECC models, including conservation goals of foraging habitats for wildlife populations.

METHODS

A foraging threshold can be defined as an amount or density of food remaining after a forager abandons feeding in a foraging patch (Brown 1988, Brown and Kotler 2004). Therefore, it is generally appropriate that food density estimates used in ECC models be reduced to account for foraging thresholds, because this food is not available to the animal due to the energetic costs of finding, handling, and processing foods exceeds energetic benefits or other factors. Corrected estimates are intended to reflect food an individual can exploit from a patch before that patch becomes unprofitable. Based on this interpretation, any incorporation of foraging thresholds into ECC estimates should be applied at the foraging patch level, which is a species- or possibly site-specific realization. Accordingly, foraging patches with food densities equal to or less than the foraging threshold would provide no profitable forage to the species of interest. Correcting average food density across a landscape of foraging patches for a foraging

threshold ($\bar{x}_{corr}$) could be described by:

$$\bar{x}_{corr} = \frac{\sum_{x_i > c}(x_i - c)}{n}$$

where x_i is the density of food within sampled forage patch i, c is the foraging threshold, and n is the total patches sampled. All patches where $x_i < c$ are not included in the summation because they have no food available for animals. More generally, patch-specific foraging thresholds may be known or could be estimated; thus, c_i could be substituted for c (van Gils et al. 2004).

Some previous bioenergetics models accounted for foraging constraints by subtracting an estimated foraging threshold from a pooled (i.e., overall) mean food density estimated by sampling multiple foraging patches (e.g., Reinecke and Loesch 1996, Central Valley Joint Venture 2006, Pearse et al. 2010). However, results employing this "mean-subtraction" method hypothetically could differ from results obtained with a patch level correction as described above. To illustrate this discrepancy, assume 3 foraging patches contained 10 units of food per ha and 3 foraging patches contained 4 units/ha (Figure 1A). If animals cease foraging in patches when food densities reached ≤6 units/ha (i.e., foraging threshold = 6), subtracting the foraging threshold from the overall mean (7 units/ha) would result in 1 unit/ha of food available per patch, on average. This value could be used to estimate total food availability if, for instance, the sample of 6 foraging patches was drawn from a population of foraging patches totaling 1,000 ha (i.e., 1,000 total food units). However, when incorporating a foraging threshold at the foraging-patch level, 3 patches would provide 4 units/ha of food (10-6=4), whereas 3 patches would intuitively provide no food (i.e., their initial value was below foraging threshold; Figure 1B). Mean food availability of all 6 sampled patches would be 2 units/ha and total food availability 2,000 units. Therefore, the mean-subtraction method underestimated mean food availability by 100% in this simple example.

The discrepancy among these two corrected means and totals reflects varying interpretations of patches with food densities below foraging threshold. For the mean-subtraction method, the constant is subtracted from the

mean, which is equivalent to subtracting that constant from each observation and then averaging the resulting values.

$$\frac{\sum_{i=1}^{n}(x_i)}{n} - c = \frac{\sum_{i=1}^{n}(x_i - c)}{n}$$

Thus, each patch with a value below a foraging threshold is included in the dataset as a negative number (Figure 1C). Negative amounts of food are illogical, whereas rounding negative values up to zero makes sense biologically, since the patch is ecologically devoid of food from foragers' perspectives. Understanding the source of these different results between methods allows prediction of magnitude and direction of bias associated with the mean-subtraction method. Both methods yield identical results if all sampled foraging patches contained food densities at or above the foraging threshold. However, when a portion of sampled patches contains less than the foraging threshold, correcting at the patch level will consistently yield greater mean food density than when subtracting a constant from the overall mean. The magnitude of difference depends on the proportion of sampled patches below foraging threshold and mean food density of sampled patches above foraging threshold.

RESULTS

Based on this discrepancy in corrected food densities, we reevaluated results from two previous studies by comparing estimates corrected for foraging threshold with both methods. Stafford et al. (2006a) estimated density of waste grain in rice fields in the Mississippi Alluvial Valley during early winter and reported rice abundance averaged 78 kg/ha across 3 years (116 kg/ha in 2000, 54 kg/ha in 2001, and 65 kg/ha in 2002). Independent studies of waterfowl foraging in flooded rice fields in this region estimated that waterfowl species wintering in the region ceased foraging when rice abundance declined to approximately 50 kg/ha, regardless of food abundance at the start of the study (Greer et al. 2009). Therefore, Stafford et al. (2006a) corrected for this foraging threshold by subtracting it from annual estimates. They concluded that rice available to waterfowl averaged 28 kg/ha overall (i.e., 66 kg/ha in 2000, 4 kg/ha in 2001, and 15 kg/ha in 2002). However, inspection of field-specific estimates of

Figure 1: Hypothetical example of 6 foraging patches containing varying amounts of food (A), where mean food density is 7 units/ha ([3×10 + 3×4] / 6). If a foraging threshold of 6 food units/ha existed, 3 foraging patches would have 4 available units/ha, 3 would have no available food (B), and adjusted mean food availability would be 2 units/ha ([3×4 + 3×0] / 6). Using the "mean-subtraction" method, the foraging threshold functionally would be subtracted from each foraging patch value (C), wherein adjusted mean food availability corrected in this manner would be 1 unit/ha ([3×4 + 3×−2] / 6).
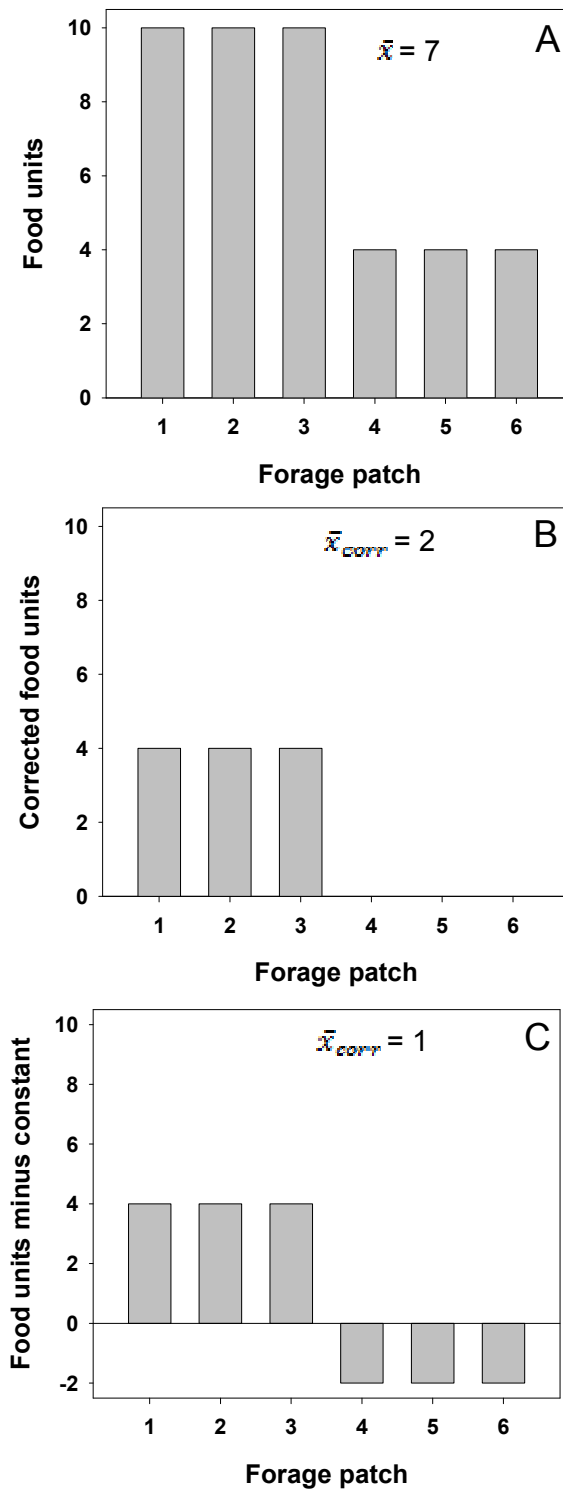
rice density revealed that 48% of sampled fields contained less rice than the foraging threshold among all study years and therefore were essentially included as negative numbers after subtracting the foraging threshold value (Stafford 2004). When correcting for foraging threshold at the field level (i.e., the best approximation of a foraging patch), we found the overall estimate of rice availability increased 59% to 45 kg/ha (73 kg/ha in 2000, 21 kg/ha in 2001, and 42 kg/ha in 2002).

Extending this example illustrates potential ramifications of error propagation in conservation planning exercises. Stafford et al. (2006a) estimated rice fields should provide 41 million duck energy-days (DEDs) for waterfowl based on an assumed forage density of 28 kg/ha (325 DED/ha). However, incorporating a foraging threshold at the patch level yielded a substantially greater estimate of food availability and hence a greater energetic carrying capacity estimate (515 DED/ha). When considered in the context of potential flooded rice agriculture during fall in this region, the revised estimate indicated rice fields would provide 65 million DEDs (24 million additional DEDs). This difference is not trivial. For example, it would require an additional 75,000 ha of flooded rice at the previously assumed value of 325 DED/ha to equal the total energetic carrying capacity value for waterfowl in the region. Manley et al. (2008) indicated the cost of providing winter wetland and waterfowl habitat in a rice-soybean rotation system would be $12.35–24.70/ha (2013 USD). Therefore, the cost of such an error would lead to the expenditure of $925,000–1,850,000 for water and infrastructure alone that may not be necessary to meet waterfowl energetic needs.

In a second case study, Pearse et al. (2010) developed an ECC model for spring staging sandhill cranes (*Grus canadensis*). They estimated density of waste corn in harvested fields in central Nebraska averaged 165 kg/ha in spring 1998 and 65 kg/ha in spring 1999. Using 6 kg/ha as a foraging threshold for cranes feeding in harvested cornfields, they subtracted this value from the aforementioned estimates and used corrected estimates of 159 and 59 kg/ha in their ECC. Field-level inspection of corn densities revealed 2 (4%) sampled fields contained less waste corn than the foraging threshold used in analyses and both occurred during spring 1998. After correcting for foraging threshold at the field level, estimated corn

availability was 160 kg/ha in 1998 and 59 kg/ha in 1999. Therefore, correction with the mean-subtraction and by field produced estimates that were identical, or nearly so, because few (1998) or no (1999) fields had seed densities below the foraging threshold.

DISCUSSION

Our examples suggest the importance of incorporating foraging thresholds or other constraints at the proper scale. For applying foraging thresholds, the appropriate scale may be at the foraging patch of the target species or the scale at which the foraging threshold was estimated. In our case studies, agricultural fields served as surrogates for foraging patches. Although convenient for sampling and experimentation, crop fields may have been larger or smaller than forage patches selected by wintering dabbling ducks or spring-staging sandhill cranes. Greater insight into how and at what spatial extent wildlife species perceive, evaluate, and select foraging patches within their environment, including influences of vegetation structure and food distribution, would be valuable for developing more realistic energetic carrying capacity models. Nonetheless, adjusting food amounts across entire landscapes, as has been done in certain foraging models used for conservation planning (e.g., Reinecke and Loesch 1996, Wilson and Esslinger 2002, Central Valley Joint Venture 2006), may have led to erroneous habitat objectives. Furthermore, inconsistency among planning regions regarding integration of foraging thresholds may lead to inefficient or ineffective inter-regional conservation planning.

Managers should be dubious of food availability estimates corrected at inappropriate or undefined scales or estimates lacking explicit methods detailing adjustment for a foraging threshold. Our findings suggest published estimates of mean food density alone will not be entirely sufficient for conservation planning purposes. In most instances, additional information will be required to adjust gross estimates for a foraging threshold. Frequency plots would be informative for determining if any patch-specific estimates were below a foraging threshold (e.g., Kross et al. 2008, Straub et al. 2012), yet providing access to data at multiple scales, potentially as supplementary appendices, would allow conservation planners to apply

foraging thresholds at the scale they deem appropriate. Multi-stage sampling may be an especially appropriate strategy for natural resource estimation, and methods are well developed to plan and optimize sampling designs to balance precision and cost (Stafford et al. 2006b).

Errors in input parameters or model structure have potential to bias overall conservation objectives and over- or under-estimate resources needed to meet objectives. Conservation objectives derived from planning models can have varying sensitivities to input parameters (Miller and Newton 1999). Thus, accurate and precise estimates are necessary to legitimize and strengthen end results. Careful evaluation of the results of conservation planning and implementation in light of potential errors in parameter estimates should be undertaken to evaluate consequences of error propagation, and plans should be revised accordingly. When input parameters are identified as influential to outcomes, collecting representative and reliable information to populate a model may be more cost effective than using 'best available' information that poorly represents the region of interest or has been collected with substandard methods. In the instance of food availability, conservation planners should take efforts to acquire estimates from probability-based sampling designs that incorporate spatial and temporal variations that are characteristic of the region in which the model is being used. Moreover, foraging threshold estimates for major foraging habitats should be determined experimentally to reduce reliance on the few published threshold values available (Greer et al. 2009, Hagy and Kaminski 2012).

Landscape-scale conservation planning establishes strategies for efficient allocation of limited monetary resources by deriving biologically defensible conservation objectives. Seemingly small errors or biases in application of input parameters, when extrapolated to large spatial extents, propagate errors that can waste limited resources or have negative implications for population growth and persistence. Our example of estimating waste-rice availability in the MAV illustrated how error propagation may have led to inefficient allocation of limited resources. In that example, bias resulted in an underestimation of carrying capacity and an overestimation of habitat need. Based on the supposition that more flooded rice fields were needed to meet overall energetic requirements of wintering waterfowl in the region, a large amount of money could

have been unnecessarily spent. Although seemingly a conservative bias in terms of habitat conservation planning, this inefficiency could have negative consequences to the target population if resources allocated to flood additional rice fields were used to manage landscapes and habitats of greater importance to populations of interest.

LITERATURE CITED

Anderson, J.T., and L.M. Smith. 1999. Carrying capacity and diel use of managed playa wetlands by nonbreeding waterbirds. *Wildlife Society Bulletin* 27:281–291.

Beck, J.L., J.M. Peek, and E.K. Strand. 2006. Estimates of elk summer range nutritional carrying capacity constrained by probabilities of habitat selection. *Journal of Wildlife Management* 70:283-294.

Brasher, M.G., J.D. Steckel, and R.J. Gates. 2007. Energetic carrying capacity of actively and passively managed wetlands for migrating ducks in Ohio. *Journal of Wildlife Management* 71:2532–2541.

Brown, J.S. 1988. Patch use as an indicator of habitat preference, predation risk, and competition. *Behavioral Ecology and Sociobiology* 22:37–47.

Brown, J.S., and B.P. Kotler. 2004. Hazardous duty pay and the foraging cost of predation. *Ecology Letters* 7:999–1014.

Central Valley Joint Venture. 2006. Central Valley Joint Venture Implementation Plan – Conserving Bird Habitat. U.S. Fish and Wildlife Service, Sacramento, CA.

DeYoung, R.W., E.C. Hellgren, T.E. Fulbright, W.F. Robbins, Jr., and I.D. Humphreys. 2000. Modeling nutritional carrying capacity for translocated desert bighorn sheep in western Texas. *Restoration Ecology* 8:57–65.

Goss-Custard, J.D., 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 Applied Ecology* 40:176–187.

Greer, D.M., B.D. Dugger, K.J. Reinecke, and M.J. Petrie. 2009. Depletion of rice as food of waterfowl wintering in the Mississippi Alluvial Valley. *Journal of Wildlife Management* 73:1125–1133.

Guthery, F.S. 1999. Energy-based carrying capacity for quails. *Journal of Wildlife Management* 63:664–674.

Haukos, D.A., and L.M. Smith. 1993. Moist-soil management of playa lakes for migrating and wintering ducks. *Journal of Wildlife Management* 21:288–298.

Heitmeyer, M.E. 1989. Agriculture/wildlife enhancement in California: The Central Valley Habitat Joint Venture. *Transactions of the North American Wildlife and Natural Resources Conference* 54:391–402.

Hobbs, N.T., D.L. Baker, J.E. Ellis, D.M. Swift, and R.A. Green. 1982. Energy- and nitrogen-based estimates of elk winter-range carrying capacity. *Journal of Wildlife Management* 46:12–21.

Kross, J., R.M. Kaminski, K.J. Reinecke, E.J. Penny, and A.T. Pearse. 2008. Moist-soil seed abundance in managed wetlands in the Mississippi Alluvial Valley. *Journal of Wildlife Management* 72:707–714.

Manley, S.W., (Ed.), 2008, *Conservation in ricelands of North America*. (Stuttgart, Arkansas, USA: Rice Foundation)

Miller, M.R., and W.E. Newton. 1999. Population energetics of northern pintails wintering in the Sacramento Valley, California. *Journal of Wildlife Management* 63:1222–1238.

Pearse, A.T., G.L. Krapu, D.A. Brandt, and P.J. Kinzel. 2010. Changes in agriculture and abundance of snow geese affect carrying capacity of sandhill cranes in Nebraska. *Journal of Wildlife Management* 74:479–488.

Reinecke, K.J., and C.R. Loesch. 1996. Integrating research and management to conserve wildfowl (Anatidae) and wetlands in the Mississippi Alluvial Valley, USA. *Gibier Faune Sauvage, Game and Wildlife* 13:927–940.

Soulliere, G.J., B.A. Potter, J.M. Coluccy, R.C. Gatti., C.L. Roy, D.R. Luukkonen, P.W. Brown, and M.W. Eichholz. 2007. Upper Mississippi River and Great Lakes Region Joint Venture Waterfowl Habitat Conservation Strategy. U.S. Fish and Wildlife Service, Fort Snelling, Minnesota, USA.

Stafford, J.D. 2004. Abundance and conservation of waste rice for wintering waterfowl in the Mississippi Alluvial Valley. Dissertation. Mississippi State University.

Stafford, J.D., R.M. Kaminski, K.J. Reinecke, and S.W. Manley. 2006a. Waste rice for waterfowl in the Mississippi Alluvial Valley. *Journal of Wildlife Management* 70:61–69.

Stafford, J.D., K.J. Reinecke, R.M. Kaminski, and P.D. Gerard. 2006b. Multi-stage sampling for large scale natural resources surveys: A case study of rice and waterfowl. *Journal of Environmental Management* 78:353–361.

Stephens, D.W., and J.R. Krebs. 1986. *Foraging theory*. Princeton University Press, Princeton, New Jersey, USA.

Straub, J.N., R.J. Gates, R.D. Schultheis, T. Yerkes, J.M. Coluccy, and J.D. Stafford. 2012. Wetland food resources for spring-migrating ducks in the Upper Mississippi River and Great Lakes Region. *Journal of Wildlife Management* 76:768–777.

van Gils, J.A., P. Edelaar, G. Escudero, and T. Piersma. 2004. Carrying capacity models should not use fixed prey density thresholds: a plea for using more tools of behavioral ecology. *Oikos* 104:197–204.

Wallmo, O.C., L.H. Carpenter, W.L. Regelin, R.B. Gill, and D.L. Baker. 1977. Evaluation of deer habitat on a nutritional basis. *Journal of Range Management* 30:122–127.

Wilson, B.C., and C.G. Esslinger. 2002. North American Waterfowl Management Plan, Gulf Coast Joint Venture: Texas Mid-Coast Initiative. North American Waterfowl Management Plan, Albuquerque, NM.

Windels, S.K., and D.G. Hewitt. 2011. Effects of plant secondary compounds on nutritional carrying capacity estimates of a browsing ungulate. *Rangeland Ecology and Management* 64:264–275.