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Analytical And Decision Tools For Wildlife Population And Habitat Management

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ANALYTICAL AND DECISION TOOLS FOR WILDLIFE POPULATION
AND HABITAT MANAGEMENT

A Dissertation Presented

by

Kurt Rinehart

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Abstract

The long-term success of wildlife conservation depends on maximizing the benefits of limited funds and data in pursuit of population and habitat objectives. The ultimate currency for wildlife management is progress toward long-term preservation of ample, wild, free wildlife populations and to this end, funds must be wisely spent and maximal use made from limited data.

Through simulation-based analyses, I evaluated the efficacy of various models for estimating population abundance from harvest data. Because managers have different estimators to choose from and can also elect to collect additional data, I compared the statistical performance of different estimation strategies (estimator + dataset) relative to the financial cost of data collection. I also performed a value of information analysis to measure the impact that different strategies have on a representative harvest management decision. The latter analysis is not based on the cost of data, but rather on the management benefit derived from basing decisions on different datasets.

Finally, I developed a hybrid modeling framework for mapping habitat quality or suitability. This framework makes efficient use of expert opinion and empirical validation data in a single, updateable statistical structure. I illustrate this method by applying it across an entire state.

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Chapter 1 Introduction and Literature Review

This dissertation explores advanced analytical methods for mapping wildlife habitat and evaluating the efficacy of competing approaches to population estimation and analysis of harvested species. I use the American black bear as a study species because resurgent populations and changing human attitudes toward bears have ushered in a new era of management for this species. The species' ecology and its potential to harm humans make its management a sensitive topic. My research is framed in the decisions facing black bear managers in choosing population monitoring programs and evaluating habitat when hard data are sparse and often prohibitively expensive to collect.

Study species

American black bears (*Ursus americanus*) once ranged across all of sub-arctic North America that had tree cover, but were extirpated across much of their range through bounties, unregulated hunting, and predator control measures (Miller 1990). In the past century, black bear populations have been afforded a number of legal protections and their populations have generally rebounded to the point that we are witnessing a new era in black bear management in North America. The current generation of managers grew up under a “recovery” regime where harvest pressure and human interference were limited in favor of natural increase. Today, recovery appears to have been successful enough in many regions that management must shift to a “maintain” regime more akin to how deer and other game species have been managed (Miller 1990).

Black bears are large-bodied, generalist omnivores that eat mostly of vegetation and hibernate in winter (Tøien et al. 2011). Adequate nutrition must be consumed in the warmer months to survive hibernation and to support reproduction (Elowe and Dodge 1989). Late summer and fall are the critical feeding periods and bears can gain up to a kilogram of mass per day when food is abundant (Jonkel and Cowan 1971).

Distribution of food and heavy cover providing refuge from human activity are the primary components of prime bear habitat (Rogers and Allen 1987, Clark et al. 1993, Mitchell et al. 2002, Pelton 2003). Wherever Black Bears are allowed to do so, they readily habituate to living alongside humans to access anthropogenic food sources such as garbage that meet the bears' need for high protein- and fat-content foods (Pelton 2003). Despite the nutritional benefits, close proximity to humans increases mortality risks to bears through legal, illegal, and accidental means (Rogers and Allen 1987, Rogers 1989, Mattson 1990). The long-term conservation of viable bear populations in the face of continued spatial expansion of humans depends on humans accepting higher risks from habituated bears and/or ensuring the existence of adequate undeveloped refugia (Mattson 1990).

Bears, especially males, may move often and range widely in search of food during late summer and fall, contributing to the greater vulnerability of male than female bears to fall hunting (Pelton 2003). Females are also less vulnerable to fall harvests because they den first, followed by sub-adults, and finally adult males (Jonkel and Cowan 1971, Johnson and Pelton 1980, Schooley et al. 1994). Winter denning typically begins between September and January and ends between March and May, depending on

latitude, with shortest periods of dormancy at the southern extent of the range (Lariviere 2001).

Black bear populations are stable or growing throughout their current North American range (Hristienko and McDonald 2007). In most jurisdictions, black bears are a managed game animal with hunting seasons typically in the fall, but also in the spring in some locales. Black bear hunting tactics include shooting over bait, calling, spot-and-stalk, stand-hunting, and pursuit with hounds. Black bears are biologically much different than deer, so their management is also different. Black bears are long-lived with low reproductive rates due to delayed female primiparity, small litters, and biennial reproduction (Pelton 2003). If subject to over-harvest, black bear populations are expected to recover less quickly than populations of other game species such as deer (Miller 1990).

Also unlike deer, black bears have greater potential to cause direct harm to humans and their property. In the past, bears mingling with human settlements might have been readily shot. Today, hunting and poaching are rarer and so bears can be afforded great latitude in exploiting human sources of food. The increasing abundances of bears, their ability to live in close among people, and the danger that they can pose in bad circumstances all counsel for management that limits their growth and proximity. On the other hand, people value knowing that bears are nearby and seeing them. This and the down-side risk of over-reducing their populations and setting back recovery unnecessarily counsels for optimality in management.

Habitat modeling

Habitat models are valuable for anticipating and assessing the impacts of environmental changes and human development on wildlife habitat (Guisan and Zimmermann 2000, Nielsen et al. 2010, Bird et al. 2011, Jackson et al. 2011). Habitat loss and degradation are leading threats to the persistence of wildlife species worldwide (Wilcove et al. 1998, Brashares et al. 2001, Schipper et al. 2008). Proper management and conservation depends on proper valuation of affected habitat, however, in many situations, adequate species-habitat data for statistical modeling do not exist.

In most cases, empirical location data can only be collected for a given species within a small geographic extent. Where these data do exist, statistical models can be fit to the data to estimate the influence of different environmental characteristics. The models, commonly called species distribution models (SDMs), include a variety of linear, nonlinear, and other forms (Elith and Graham 2009) that typically exploit locations of species detections, without or without accounting for imperfect observability (e.g., MacKenzie et al. 2003, Phillips et al. 2006). Increasingly, researchers and conservationists are taking account of spatial-autocorrelation (Fortin and Dale 2009, Fotheringham 2009) and using spatially-explicit models for analyzing species distributions (Augustin et al. 1996, Lichstein et al. 2002, Dormann et al. 2007, Fortin and Dale 2009, Carroll et al. 2010). All of these methods require empirical location data and are therefore, usually limited to application in relatively small, disparate locations.

Habitat suitability index models

Habitat Suitability Index (HSI) models (USFWS 1980, 1981) are theoretical, deductive models designed to model habitat when no adequate empirical data are available. HSI models consist of input variables (e.g., distance to roads, percent of habitat in the surrounding area), suitability functions (e.g., linear equations) that specify the change in suitability as input variable changes, and an aggregating scheme for combining the individual suitability indices into a single HSI value per spatial unit. Identification of each of these components depends on published literature and expert opinion.

HSI modeling requires expert judgment to identify variables and create suitability functions. In some cases, these functions are estimated, but this requires some amount of empirical location data (e.g., Powell et al. 1997). More commonly, suitability functions are “built by hand” through an iterative process of educated guessing and visual and mensurative calibration with independent data (Brooks 1997). Sometimes individuals build the functions and sometimes groups. In a group model, discrepancy between experts’ judgments (between-expert uncertainty) can be the dominant source of uncertainty in the model (Czembor et al. 2011). Forced consensus is prone to social and cognitive biases, particularly over-confidence (Clemen and Winkler 1999, Kahneman et al. 1999, Burgman 2005). By extension, different individuals are expected to build their models differently as well. Attempts to characterize the uncertainty of deductive models involve Monte Carlo simulations (Bender et al. 1996, Frey and Rhodes 1996), but such exhaustive treatments ignore experience and prior knowledge and will be a practical impossibility in many cases (Ferson 1996).

The steps of building an HSI model include calibration, verification and validation (Brooks 1997). Calibration and verification include referring to external information to test that components of the model are behaving as intended. A common means of calibration is applying a new model to a familiar landscape to see that the results conform to reasonable expectation and that the modeled HSIs span the reasonable range of values, allowing for relevant distinction between sites. Verification consists of a more general assessment of model construction including how well the modeled HSI tracks other putative measures of quality—that “good” areas have higher HSIs than “bad” areas.

Validation is the final, critical step before one should use an HSI for its intended purpose (Brooks 1997, Roloff and Kernohan 1999). Validation requires comparison of the HSI output to some independent data representing the ecological process of interest, such as location, reproductive, or abundance data (Kilgo et al. 2002, Mitchell et al. 2002, Tirpak et al. 2009, Jones-Farrand et al. 2011). The information gleaned from the comparison of the HSI model to this other information is the basis of confidence in its use. However, no rigorous method exists for integrating the new knowledge into the existing model form and any alterations to the HSI model must be ad hoc (McLaughlin 1999, Mitchell et al. 2002).

My research attempts to streamline model-building by formulating expert opinion in a manner that is amenable to the same statistical models that we use for empirical location data. This offers several advantages in terms of simplified model formulation, rigorous validation with automatic updating of model parameters, and a generalizable structure that can be used and adapted across broad regions.

Population estimation

A wildlife manager's choice of estimator must take into consideration data collection costs, particularly where additional data may make a viable choice of an otherwise unsuitable estimator. Examples of datasets that may accompany the age-at-harvest data include tag sales, the hunter participation rate (the proportion of hunters who actively hunt, given a tag was purchased), and the hours spent actively hunting per participant. Additionally, mark-recapture datasets permit estimation of harvest and survival rates.

From the manager's perspective, the choice of which estimator is optimal likely depends on three critical objectives: minimizing the bias (the difference between the estimated abundance and true abundance), maximizing precision (shrinking the confidence interval of the estimate), and minimizing cost (the cost of the data needed for population estimation). New analytical methods are continually being developed (Skalski et al. 2005), presenting managers with an ever-increasing number of options for estimating the size or trend of a harvested population.

I examined three different population estimators in the course of my research, the Downing population reconstruction (Downing 1980), the Paloheimo-Fraser successive sex ratio estimator (Paloheimo and Fraser 1981), and statistical population reconstruction (e.g., Gove et al. 2002, Gast 2012). The first two techniques are commonly used in the management of black bears and the latter has been applied to black bear populations in the literature (Conn et al. 2008) and offers promise for managers.

Population reconstruction

Population reconstruction methods were first developed for use in fisheries where samples (e.g. commercial net captures) included large numbers of individuals that could be sorted into age classes according to length. These methods are variously known as stock assessments, virtual population analysis, cohort analysis, and, particularly in terrestrial species, population reconstruction. Population reconstruction generally aims to estimate the pre-harvest abundance in a given year. The annual cycle is characterized by a period where all mortality is a function of the harvest and a second period in which all mortality is from natural causes. The post-harvest abundance P_t , is

$$P_t = N_t - H_t,$$

$$H_t = N_t * h_t.$$

where the post-harvest abundance is the pre-harvest abundance (N_t) less the number of animals harvested, H_t , which is the product of N_t and the harvest rate, h_t . The estimate of the pre-harvest abundance in the following year is then

$$N_{t+1} = P_t * s_t,$$

the post-harvest abundance discounted by the rate of survival, s_t , from time t to $t+1$. A single, simplified formula for this is

$$N_{t+1} = s_t(N_t - H_t),$$

which can be re-arranged to the essential reconstruction equation

$$N_t = \frac{N_{t+1}}{s_t} + H_t.$$

If harvest and natural mortality are not differentiated, then the survival rate from time t to $t+1$ is presumed to include all harvest mortality, so the equation simplifies to

$$N_t = \frac{N_{t+1}}{s_t}.$$

Population reconstruction is often referred to as “backwards accounting” because the information about abundance in time $t+1$ is used to calculate that of time t . The differences among reconstruction methods largely depend on the means of estimating the s_t , or more commonly the mortality rate, $1-s_t$.

The Downing reconstruction (1980) is one of the simplest methods, and it is also one of the most commonly-used for terrestrial wildlife management. In Downing’s seminal application, he used the data published by Robinette et al. (1977) from an intensive study of a deer herd living on a 137 km² study area. Those authors accounted as well as possible for all sources of mortality, so the data used by Downing are more likely to approach an accurate estimate of abundance than a table based solely on harvest data, which will be negatively biased because not all mortality will be included in the calculations.

Reconstruction calculations work backwards through a cohort (a group of animals born in the same year). One of the issues with population reconstruction is the difference between ‘complete’ and ‘incomplete’ cohorts. A cohort is ‘complete’ when it is entirely represented in the mortality data. That is, if the terminal age is 15 years, then a complete cohort is one that has mortality counts for all ages up to and including 15 (the final age class is considered terminal, meaning no individuals survive beyond it). Backwards

reconstructions cannot be made for incomplete cohorts, so for long-lived animals, this means that mortality counts must be collected for many, many years in order to get sufficient complete cohorts to make meaningful reconstructions.

Another way to solve this problem is to use “terminal age-class pooling” and Downing has been shown to be robust to this practice (Davis et al. 2007; Rinehart, unpublished data). Terminal age-class pooling simply means that for the population with a terminal age of 15, we can pool ages 10-15 (for example), into a new terminal class called “10+”. Such pooling does not alter the reconstruction of the completed cohorts, and it makes more completed cohorts out of the same dataset, as any cohort having attained at least 10 years of age in the dataset is now “complete”. The only limitation is that the final 2 age classes, the “plus” class and the one preceding it (e.g. age classes 9 and 10+) must contain adults with equal mortality rates. This equal rates assumption is the key to Downing’s method.

Given consistent mortality across the final two age classes, the first step in the Downing reconstruction is to estimate the adult mortality rate (the following calculations are summarized in Table 1.1). For an illustrative example, let us assume that the 2 adult classes are 2.5 year olds and 3.5+ year olds. The first step is to find the average annual mortality for each of the final age classes. In order to begin the reconstruction with the existing data, Downing uses “average” values to project information into a hypothetical “final+1” year of data, a point from which to reconstruct backwards into the final year of the actual data. In our example, the average mortality in the final 2 classes is 108.2 and 74.7, respectively. Now we can reason that any animals that die as 3.5+ must have survived being 2.5. Similarly, any animals that die as 2.5 must have previously been

alive. Therefore, a rough estimate of adult survival rate is the ratio of the average 3.5+ class mortality to the 2.5 class mortality. We can construe this as a mortality rate by taking 1 minus this ratio:

$$m = 1 - \frac{C_{3.5+}}{(C_{2.5} + C_{3.5+})}$$

where m is the mortality rate for adult age classes and C_i is the mortality count for age class a . In our example, the mortality rate, figured for the average counts, is 0.59 ($1 - 74.7/108.2$). Given the preceding assumption of constant mortality rate across these two age classes, we can then use this one rate to reconstruct an estimate of the abundance in the final year of the data. The reconstructed abundance for a given adult age class is found as

$$R_{a,t+1} = \frac{C_{a,t}}{m_t}$$

where $R_{a,t+1}$ is the reconstructed abundance for age class a and time $t+1$. Applying the mortality rate of 0.59 to mortality counts of 108 and 73 leads to abundance estimates of 183 and 126, for the 2.5 and 3.5+ classes, respectively.

The values calculated above are the “final+1” year estimates of abundance for the adult classes. With these in place, we can employ a similar practice to reconstruct abundance for the adult classes in all years of data. Now, the adult survival rate is computed as the sum of mortality counts for the last two classes in a given year plus the 3.5+ abundance in the following year

$$m_t = 1 - \frac{R_{3.5+,t+1}}{(C_{2.5,t} + C_{3.5+,t} + R_{3.5+,t+1})}$$

This formula shows that our estimate of survival rate is the number of adults surviving time t divided by all the adult animals that had to have been alive that time. The reconstructed abundance of older adults in time $t+1$ includes all adult survivors of time t . To this we add all those that died in time t to get the total that must have been alive. When working on the final year of mortality data, we make use of the hypothetical data for time “final+1” that we generated above. By employing the formula above in the basic reconstruction formula ($R = C/m$), the abundances for the final two age classes can be reconstructed for all years of data. Of course, 1 minus the survival rate yields the mortality rate.

Once the adult classes are reconstructed, the younger age classes for all cells can be reconstructed by simple back-wards addition, within a cohort, of harvest counts with the reconstructed abundance in the following year

$$R_{i-1,t} = R_{i,t+1} + C_{i-1}$$

where the subscript i takes a maximum value equal to the younger of the two adult age classes.

Annual abundance estimates are the sum of the age-specific reconstructed abundances for each year. Reconstruction is performed separately for the sexes and then the results are combined to arrive at total population estimates. The final years of data include incomplete cohorts for which the reconstructions are merely backwards addition of harvest counts and are strongly negatively biased. The number of years with

incomplete cohorts is a function of the number of age classes used. Recall that adult classes can be pooled to just 2 classes to minimize the impact of incomplete cohorts.

The Downing method has been subject to several performance assessments (Davis et al. 2007, Fieberg et al. 2010) and is known to be a negatively-biased abundance estimator. This negative bias is accentuated when only harvest counts are used instead of total mortality counts. The assumptions of the Downing reconstruction as typically applied to harvest counts are that the ratio of harvest mortality to total mortality is constant across cohorts, that the mortality rates of the terminal 2 adult age classes are equal, and that age distributions in the reported mortalities are unbiased samples of the population age distribution.

Davis et al. recorded a 10-20% negative bias in abundance estimates, but the degree of bias will be a function of the number of animals dying without record. When natural mortality is low, (e.g. adult black bears), the bias will be low. Davis et al. assumed low natural mortality rates (e.g. ~10%). These rates are consistent with research on adults (Bunnell and Tait 1985, Beston 2011), but research also shows sub-adult and yearling black bears can have natural mortality rates up to 30% (Beston 2011). Higher natural mortality among age classes that can be abundant in the harvest counts would be expected to contribute to even greater negative bias to abundance estimates.

Statistical population reconstruction

The primary difference between various versions of population reconstruction is the means by which mortality rates are estimated. In the simplest methods, the mortality estimate is just the ratio of reported mortality to the back-calculated abundance for a

given age and year (Fry 1949). Downing constructs the two terminal age classes as having constant rates and estimates mortality using a similar ratio of mortality count over a sum of mortalities and reconstructed abundances (Downing 1980). More sophisticated methods suppose that the ratio of harvest to abundance is a non-linear function of instantaneous harvest and mortality rates (Gulland 1965 and Pope 1972, c.f. Skalski et al 2005). These non-linear reconstructions are more realistic in their modeling of harvest processes, but they require initial estimates of harvest rate of the terminal (oldest) age class and the annual instantaneous natural mortality rate. Another means of generating plausible estimates of harvest mortality rates is to use auxiliary information for guidance. Fryxell et al. (1988) estimate harvest rates as a function of hunter effort. Statistical population reconstruction is the logical extension of this practice: using auxiliary information to support statistical estimation of the rates used to reconstruct abundance.

Statistical population reconstruction (SPR) is a class of population estimators that are similar to classic population reconstruction techniques, but use auxiliary data to estimate nuisance parameters that cannot be estimated from harvest data alone. The fundamental feature of SPR is the marriage of age-at-harvest data and auxiliary data within a statistical model to jointly estimate the required quantities. This has the benefit of relaxing the assumptions that are required for non-statistical reconstruction as well as allowing rigorous estimates of uncertainty. The auxiliary data used for published examples of SPR include hunter effort data (Skalski et al. 2007, Fieberg et al. 2010, Skalski et al. 2011), vegetation impact data to index deer abundance (Skalski et al. 2007), wildlife food availability (Fieberg et al. 2010), wildlife sighting rates (Gast 2012), and recoveries of tagged animals (Gove et al. 2002, Conn et al. 2008, Broms et al. 2010,

Fieberg et al. 2010). SPR methods can also include models for errors associated with data such as age classifications (Conn et al. 2008).

The abundance of a given age class of animals in a given year is modeled as the abundance in the previous year and age-class (i.e., within the cohort) less those individuals harvested or dying of natural causes. Harvest and non-harvest mortality are confounded in normal reconstruction, but if one models survival using another dataset, then the identification and estimation of these rates is possible. Gast (2012, 2013) assessed the statistical performance of various forms of SPR, including some with and without random effects and recruitment functions. The best-performer in his study, which Gast called the Horvitz-Thompson-type estimator, estimated only harvest vulnerability and survival (Gast et al. 2013). This model was so-named because it does not estimate abundance directly, but does so indirectly as

$$\hat{N}_i = \frac{\sum_{j=1}^A C_{ij}}{\hat{h}_i},$$

which states that the estimated abundance (\hat{N}_i) for year i is the sum of the harvest counts for that year divided by estimated annual harvest rate. This formula, which we have also used above, mimics the Horvitz-Thompson estimator (Horvitz and Thompson 1952), except it uses an estimated rate in the denominator rather than a known one, hence Gast's use of the modifier "-type". Gast's Horvitz-Thompson-type estimator follows the form shown below for a 3 age-class example. The likelihood of being harvested in a given year is constructed as being conditional upon being harvested at all, hence the likelihood of the harvest and survival rates, h and s given the harvest counts for cohort A is

$$L(h, s \mid \vec{C}_A) = \left(\frac{\sum_i C_{ii}}{C_{11}C_{22} \dots C_{ij}} \right) \left(\frac{h_1}{h_e} \right)^{C_{11}} \left(\frac{(1-h_1)s_1h_2}{h_e} \right)^{C_{22}} \left(\frac{(1-h_1)(1-h_2)s_2h_3}{h_e} \right)^{C_{33}}$$

where C_{ij} are the harvest counts at age i in year j and h_e , the probability of ever being harvested, is

$$h_e = h_1 + (1-h_1)s_1h_2 + (1-h_1)(1-h_2)s_2h_3.$$

Supposing that the auxiliary data consist of counts of tagged animals, the auxiliary likelihood for harvest and survival rates could take the form

$$L(h, s \mid r, t, d) = \prod_{i=1}^Y \binom{r_i}{t_i, d_i} h_i^{t_i} [(1-h_i)(1-s_i)]^{d_i} [(1-h_i)s_i]^{r_i-t_i-d_i}$$

where r_i is the number of tagged animals at risk, t_i is the number of tagged animals that were harvested, and d_i is those tagged animals that died of non-harvest causes in year i .

Then the joint likelihood is

$$L_{joint}(h, s \mid C, r, t, d) = L_{age-sex \text{ at harvest}} * L_{auxiliary}$$

Estimation of the model can be performed in several ways including Maximum likelihood and Bayesian formulations. Harvest rates are often modeled as

$$h_i = 1 - e^{-v*fi}$$

where v is the vulnerability of the species to harvest and f is the annual hunter effort. This model form is common in other population estimation methods and is particularly useful when auxiliary data on hunter effort are available. Logistic functions are commonly used for rates, but are not recommended for SPR (Skalski et al. 2012). If rates (e.g. survival)

are modeled without link functions, then estimation outside of reasonable bounds provides information about structural model-fitting problems. Diagnostics based on consultation of Anscombe residuals and subsetting of the data are also recommended to evaluate model fit (Skalski et al. 2012). As with traditional reconstruction methods, the analysis is performed on each sex separately and the results are added together.

Successive sex ratio estimator

In wildlife populations, it is common for one sex to be more vulnerable to harvest than the other. When this situation occurs, then the expected sex ratio in the harvest will shift over time as the more vulnerable sex is depleted from the population. Paloheimo and Fraser (1981) and Fraser et al (1982) exploited this relationship to estimate sex-specific harvest rates which would be used to reconstruct the population abundance as the harvest count divided by the harvest rate. Given a dataset that shows the count of males and females of all age classes harvested in a given year, there exists a harvest sex ratio for every age class. The basis of the Paloheimo-Fraser (PF) model is a non-linear regression of the natural logarithm of sex ratio onto the age classes. With harvest counts and effort data from a cohort over all the years they are in the harvest, one can regress the harvest sex ratio on the age classes to estimate the per-effort harvest vulnerability over time.

The PF regression model is parameterized such that the harvest count for each sex is a function of the effort expended during the hunting season. In order to estimate harvest rates for both sexes as independent quantities, they estimate two vulnerability parameters, p and u . The per-effort vulnerability, v , is given by $p-u$ for females and $p+u$ for males, with the harvest rate

$$h_{s,i} = 1 - e^{-v_s * f_i}$$

where $h_{s,i}$ is the harvest rate for sex s in year i , e is the base of the natural logarithm, v_s is the sex-specific vulnerability coefficient, and f_i is the hunting effort in year i . The expected harvest sex ratio in year i is

$$E \left[\frac{H_{m,i}}{H_{f,i}} \right] = R_0 * \frac{h_m * e^{-v_m * g_i}}{h_f * e^{-v_f * g_i}}$$

where R_0 is the sex ratio at birth and g_i is the cumulative hunter effort since the cohort was first part of the harvest. Therefore, the harvest sex ratio is a function of the initial sex ratio and the progressive depletions over time. If the birth sex ratio can be assumed to be 1:1, then that term can be dropped from the equation. In practice, weighted non-linear least squares is used to fit a regression model to the natural logarithm of the sex ratios using an appropriate rearrangement of the formula above.

The PF model requires the assumptions that 1) harvests are an unbiased sample of sex ratios, 2) the vulnerabilities of each sex are constant over time and age classes, 3) fluctuations in harvest mortality are solely a function of effort, 4) annual harvest effort is known, 5) natural survival is equal across the sexes, and 6) the population is demographically closed. Although originally proposed for analysis of harvest counts of an individual cohort over time, with the additional assumption of stable and stationary population, the method can be applied to the harvest counts across ages in a single year.

Harris and Metzgar (1987) analyzed of the performance of the Paloheimo-Fraser method under violations of the method's key assumptions: Both sexes equally abundant in the age class prior to the youngest age class in the harvest (or that sex ratios are

empirically known); no systematic changes in sex-specific vulnerability occur with increasing age; and differential vulnerability to harvest as the only factor influencing sex ratios. They found the models sensitive to violations of each of the assumptions and strongly cautioned users of these methods, but this estimator requires only harvest data and effort data, so it is an attractive option for many situations.

The PF method is used to estimate black bear populations in several jurisdictions, including Vermont and New Hampshire. In these two states, which typically have low inter-annual variability in effort, hunter effort data are replaced with a constant value that represents an estimate of the average effort in a given year. (pers. comm. K. Gustafson, NH Fish and Game). The results appear sensible and consistent with interpretation of other information, but I know of no rigorous examination of the effect of this adaptation on the functioning of the model.

Evaluating population estimators

A manager's choice of population estimator is generally seen as being determined by the available data. This same situation can also be seen in a decision context as representing the choice between current data and applicable methods or the collection of additional data that may support a different set of estimators. Any choice of estimator should consider the costs and benefits of additional data. To that end, my research examined this question directly by incorporating cost estimates for various datasets and analyzing them using the above methods. The result allows managers to examine statistical gain relative to financial costs. I further employed value of information analysis

to identify the value of each estimator and various datasets in terms of the harvest management decisions that they are intended to serve.

Wildlife and conservation managers, in particular, are often faced with the two jobs of monitoring and managing for conservation. Monitoring can be difficult and costly, and any dollars spent on monitoring cannot be spent on any other activities, despite the fact that monitoring does not accomplish conservation. Increasingly, researchers are focusing on the relative benefits of monitoring expenditures (e.g., Field et al. 2005). Generally, monitoring is most valuable when existing information is highly uncertain and influential to decision outcomes (Hauser et al. 2006, Mäntyniemi et al. 2009). Explicit, up-front costs of monitoring (“information-gathering”) can alter management plans when included in management planning (Moore and McCarthy 2010). Considerable research has been devoted to “how” best to monitor, but whether and when the information is worth it has been studied less. McDonald-Madden et al (2010) present a basic framework for managers to evaluate whether dollars spent on monitoring contribute efficiently to conservation objectives. In reality, some decisions are robust to uncertainty (e.g., Boyce et al. 2012) and the cost of additional information can greatly outstrip its value to managers. The costs and benefits of data and analysis are worthy of scrutiny, especially when monitoring and management are funded from a common resource pool. Within the monitoring-management construct (setting aside consideration of “research” pursuits), what matters is the value that the information can deliver in terms of the decisions faced by managers.

Value of information analysis (VOI; Raiffa and Schlaifer 1961) is a technique of decision analysis that addresses directly the value to be gained by applying information to

the uncertainties in a decision problem. This analysis has been employed widely in fields such as risk analysis, economics, industrial production, and medicine (e.g., Yokota et al. 2004, Yokota and Thompson 2004, Bienstock and Royne 2007, Brennan and Kharroubi 2007, Chernew et al. 2008, von Winterfeldt et al. 2012, Willan et al. 2012). Felli and Hazen (1998) demonstrate the particular strength of VOI (specifically, expected value of perfect information, see below for details) in their application to sensitivity analysis. Those authors demonstrate that other methods of sensitivity analysis can indicate the probability of a decision change as information changes, but only VOI also accounts for the marginal benefit of the change. VOI allows the decision-maker to see how much better an outcome may be possible and what it will cost to achieve it. Increasingly, these methods are being adopted in conservation, a field with chronic uncertainties that impact decision-making (e.g., Polasky and Solow 2001, Ritchie et al. 2004, Mäntyniemi et al. 2009, Williams et al. 2011, Moore and Runge 2012, Johnson et al. 2014).

The value of information is entwined with expected value decision-making, which posits that the expected value of a decision alternative is the probability-weighted sum of the possible outcomes. If you could win \$100 or lose \$50 on the flip of a fair coin, the expected value of that event is \$25 ($25 = 0.5 \cdot 100 + 0.5 \cdot -50$). In that case, the randomness of the coin determines the outcome, but in other situations, the obstacle is an uncertain state, not randomness. If you are invited to join an exciting start-up company, the ultimate outcome (payoff) to you depends on whether the company will succeed or not. That may not be random, but it will be unknown. The same situation is faced by wildlife managers that must choose management actions such as opening or closing hunting seasons, transplanting animals, captive breeding, etc. Their successes will depend

on many things that will not be purely random and will not be clearly known when the decision must be made. In that case, they must do their best to evaluate which option offers the maximum expected value, given the uncertainties involved.

The value of information is captured in how it changes the expected value of the decision outcome by reducing relevant uncertainty. In practice, not all uncertainty, if resolved, will change a decision outcome. Where multiple uncertainties exist, VOI facilitates identification of the most costly uncertainties (Runge et al. 2011) and can aid in identifying robust management strategies (Moore and Runge 2012, Johnson et al. 2014). As a result, VOI can be a helpful tool in designing survey protocols well in advance of decision-making (Polasky and Solow 2001, Johnson et al. 2014). Adaptive management, a formal program of integrated monitoring and decision-making over time intended to jointly pursue management objectives and reduce scientific uncertainty, is often prescribed for management of and within ecological systems typified by imperfect observability and high structural uncertainty because it offers the benefits of learning while managing. Williams, et al (2011) extend the application of VOI to the iterative monitoring and managing decisions inherent in adaptive management and recommend continued and more focused application of this analysis in the future.

I applied VOI in my evaluation of the efficiency of various population estimators and whether the collection of additional information contributes to better management outcomes. The following section introduces key elements of value of information analysis and walks through an example of the value of information analysis I employ in a later chapter.

Consider a simple harvest management decision with the objective of maintaining the population near a target abundance level. That target abundance has been identified by relating contemporaneous abundance estimates and relevant wildlife management objectives such as ample harvest and observation opportunities and acceptable levels of wildlife-caused nuisance or damage. The decision alternatives include whether to increase (“INCR”), decrease (“DECR”), or maintain (“STAY”) current harvest through some defined sets of actions such as changing the number of tags available or the length of the hunting season. The states of the population are whether it is above (“trueHI”), at (“trueAT”), or below (“trueLO”) the determined target. The payoff value of each alternative depends on the true state of the population.

Payoff values

Decision analysis requires some means of measuring the value obtained by the decision. In economic applications, decisions can be valued as dollars, with some alternatives yielding gains (positive values) and others, losses (negative values). When natural measures (e.g. dollars) are not available, arbitrary values can be used (e.g., Runge et al. 2011). I assigned arbitrary values to the outcomes of the harvest management example such that desirable outcomes have positive values of 100 and undesirable outcomes take negative values between -25 and -100 (Table 1.2).

Note that the payoff matrix for this example is asymmetric. The values are scaled with a bias against over-reduction of the population. That is, decreasing harvest on an overly large population ($V[\text{DECR given trueHI}] = -50$) is less bad than increasing harvest on a small population ($V[\text{INCR given trueLO}] = -100$). Both cases might move the

population equally far from the target, but these payoff values include additional “loss” associated with driving a population down as opposed to up, a potentially meaningful distinction in population management.

Expected value decision-making

A simple strategy for decision-making in the face of uncertainty is to select the alternative that maximizes the expected value of the outcome. The expected value can be thought of as the average value you could obtain over many iterations of the decision. The calculation requires the state-dependent payoff values of the alternatives and some estimate of the probabilities of occurrence of the system states and of the payoffs for each alternative given each state. The expected value of a given alternative is

$$EV(Alternative_a) = \sum_{i=1}^S P(state_i) * V(Alternative_a|state_i)$$

where $P(state_i)$ is the probability of occurrence of state i , $V(Alternative_a / state_i)$ is the payoff value of alternative a when state i occurs, and S is the total number of possible states. The state probabilities that are used in this calculation are called “prior” probabilities because we must know them prior to the analysis. The optimal decision for a purely rational, risk-neutral decision-maker is the alternative with the maximum expected value:

$$EV_{prior} = \max_a \left[\sum_{i=1}^S P(state_i) * V(Alternative_a|state_i) \right].$$

The qualifier “prior” denotes that the decision-maker has no means of reducing the state uncertainty and so makes a simple assessment of which alternative will deliver the maximum expected value.

Suppose we have existing information that suggests the following prior state probabilities: $P(\text{trueHI}) = 0.25$, $P(\text{trueAT}) = 0.50$, and $P(\text{trueLO}) = 0.25$. Using the payoff matrix in Table 1.2, the expected values of the three alternatives are:

$$EV(\text{INCR}) = 0.25 * 100 + 0.5 * -50 + 0.25 * -100 = -25$$

$$EV(\text{STAY}) = 0.25 * -25 + 0.5 * 100 + 0.25 * -50 = 31.25$$

$$EV(\text{DECR}) = 0.25 * -50 + 0.5 * -25 + 0.25 * 100 = 0.$$

The STAY alternative offers the maximum expected value; it would give the maximum average payoff if this decision were made over and over again. Theoretically, over many iterations of identical decisions, STAY will earn -25 one quarter of the time, 100 half of the time, and -50 one quarter of the time. This would lead to average payoff per decision of 31.25. Based on the given state probabilities, the optimal decision would yield $EV_{\text{prior}} = 31.25$ by choosing STAY.

If no prior information exists as to the state probabilities, then we could make them all equal: $P(\text{trueHI}) = P(\text{trueAT}) = P(\text{trueLO}) = 1/3$. This is the conventional “uninformative prior” probability distribution indicating no belief in one state being more likely than another. In this case, the expected values will change to:

$$EV(\text{INCR}) = 0.33 * 100 + 0.33 * -50 + 0.33 * -100 = -16.67$$

$$EV(\text{STAY}) = 0.33 * -25 + 0.33 * 100 + 0.33 * -50 = 8.33$$

$$EV(\text{DECR}) = 0.33 * -50 + 0.33 * -25 + 0.33 * 100 = 8.33.$$

Now the expected values of STAY and DECR are equal. A purely rational, risk-neutral decision-maker would be ambivalent between these two alternatives, both of which deliver $EV_{\text{prior}} = 8.33$. Note that in this case of maximum uncertainty about state probabilities, the expected values are very low compared to the maximum potential payoffs of 100, even lower than in the previous example. The decision-maker is blind to the true state, so he must simply choose one alternative to employ and because it “wins” sometimes and “loses” sometimes, the high potential payoff values are eroded.

Expected value of perfect information

One way to assess how uncertainty erodes decision outcome value is by calculating the expected value of perfect information (EVPI), how much additional value you could capture if you were able to resolve the state uncertainty. Imagine now that you had some perfect “test” of the uncertain population state. The term test is used generically to mean some method of inference that serves to classify, identify, or “diagnose” the true state of the system; it does not necessarily mean a statistical hypothesis test. In population management, that typically means inference of the population state based on some data. In the case of perfect information, we can somehow know the population state exactly. If the test shows the true state to be above the target, then you would choose the INCR alternative, the one that gives the maximum outcome value for that state ($V[\text{INCR} | \text{trueHI}] = 100$). Likewise, applying a perfect test would allow you to obtain the maximum outcome value for any state. The perfect information does not change the variety of the states or the distribution of their probabilities, it merely allows the decision-maker to

know which state prevails in a given instance so that he can choose the best-suited alternative. Using the expected value convention, we can now calculate the expected value *given* perfect information (EV|PI) as the sum of the maximum possible outcomes for each state times the probabilities of occurrence of the states:

$$EV|PI = \sum_{i=1}^s P(state_i) * Max [V(state_i)],$$

where $Max[V(state_i)]$ is the maximum payoff value associated with state i , regardless of alternative. Consulting the payoff matrix for this example (Table 1.2), we see that the payoff values for the state trueHI are 100, -25, and -50, with a maximum of 100. If we knew that the state was trueHI, we could choose an alternative (INCR) to obtain a payoff of 100. Similarly, the maximum payoffs under the other states (by selecting different alternatives) are also 100. Using the uniform state probabilities, EV|PI is

$$EV|PI = 0.33 * 100 + 0.33 * 100 + 0.33 * 100 = 100.$$

If we could completely remove the state uncertainty, we could expect to earn an average payoff of 100. The difference between this value and the EV_{prior} is the expected value *of* perfect information (EVPI), the value that is lost due to state uncertainty. Again using the uniform state probabilities, the EVPI is

$$EVPI = 100 - 8.33 = 91.67.$$

When payoffs are in dollars, EVPI is interpreted as the amount one would be willing to pay to reduce the state uncertainty. Although this example is not suited to that interpretation, we can see that the state uncertainty accounts fully for the 92% loss of

value from the perfect case to the simple case. Unfortunately, there is no way to truly have “perfect” knowledge of uncertain states such as these.

Sample information

Although no information will ever be perfectly certain, measures do exist that can deliver imperfect knowledge and reduce at least some of the uncertainty impacting the decision. In harvest management, perfect information would be instantaneous knowledge of all individuals in the population. That is impossible, but we can *sample* the population and derive some knowledge that may help us reduce state uncertainty. The expected value of sample information (EVSI; also called expected value of imperfect information, EVII) is the measure of how inferences based on a sample can affect our decision outcome expectations. With EVSI, we accept that our “test” (e.g. population monitoring) will be imperfect, and we account for that probabilistically. In a sense, we want to know something about the probability that the test is correct. In a 3-state system, we can’t simply ask when the test is correct, because our test can be “wrong” in two different ways. The system has three states (trueHI, trueAT, and trueLO) and the test has three possible results (testHI, testAT, testLO). We want to know the probability of each test result given each of the true states ($P(\text{testHI} \mid \text{trueHI})$, $P(\text{testAT} \mid \text{trueHI})$, etc.), for all combinations of the three potential test results and the three system states (Table 1.3**Error! Reference source not found.**). These probabilities are discovered through research that must be undertaken prior to this analysis. For reasons made clear in the next section, this is called “pre-posterior analysis” (Yokota and Thompson 2004).

Bayes' theorem

The conditional probabilities described above tell us the probability of a *result given a state*, $P(\text{result} | \text{state})$. Knowing the state, we could make a guess as to what result we will see from a given test. However, the inability to know that state is exactly the problem plaguing the decision-maker. What we really want to know is the probability of a *state given a test result*. Let us look first at just a single test result, testHI. When we assess the population and obtain a result of testHI, we can use Bayes' Theorem to compute the probability of the various states:

$$P(\text{state}_i | \text{testHI}) = \frac{P(\text{testHI} | \text{state}_i)P(\text{state}_i)}{\sum_j P(\text{testHI} | \text{state}_j)P(\text{state}_j)}.$$

The left-hand side of the equation is what we want to know, the probability of the state given the result. This is the “posterior” state probability, the prior state probability “updated” with the sample information. On the right-hand side, the prior probability of state i , $P(\text{state}_i)$, is multiplied by $P(\text{testHI} | \text{state}_i)$, the conditional probability of result testHI, given state i . In common terms, this is also referred to as the “likelihood” of observing the data under hypothesis i . The product of these quantities is the joint probability of the result and the state co-occurring (Table 1.4). The denominator is the sum of the joint probabilities for testHI across all states, which is also equivalent to $P(\text{testHI})$, the unconditional probability of the result testHI.

So for the result testHI, the joint probabilities for each state are (**Error!**

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$$P(\text{test HI \& trueHI}) = 0.33 * 0.80 = 0.267$$

$$P(\text{test HI \& trueAT}) = 0.33 * 0.05 = 0.017$$

$$P(\text{test HI \& trueLO}) = 0.33 * 0.03 = 0.01.$$

The sum of these joint probabilities is the P(testHI), 0.293. This allows us to calculate the posterior probabilities (**Error! Reference source not found.**) of the states given the result of testHI:

$$P(\text{trueHI} | \text{testHI}) = 0.267 / 0.293 = 0.91$$

$$P(\text{trueAT} | \text{testHI}) = 0.017 / 0.293 = 0.06$$

$$P(\text{trueLO} | \text{testHI}) = 0.01 / 0.293 = 0.03$$

Expected value of sample information

Once we have obtained the posterior probabilities, we can proceed with the analysis of how sample information reduces uncertainty and increases the expected value of our decision. The conceptual model of EVSI is as follows: before making the decision, the decision-maker makes an inference based on sample information. Here we use the convention of performing a “test” with three possible results to diagnose the true state. Suppose the population test gives a result of testHI. Now we approach the decision as a choice among the existing alternatives, each with a state-dependent payoff that will occur according to the posterior probabilities of the states given testHI:

$$EV(\text{Alternative}_a | \text{result} = \text{testHI})$$

$$= \sum_{i=1}^S P(\text{state}_i | \text{testHI}) * V(\text{Alternative}_a | \text{state}_i)$$

Which, using values from Table 1.2 and Table 1.5, looks like this in our example:

$$EV(\text{INCR} \mid \text{testHI}) = 0.91 * 100 + 0.06 * -50 + 0.03 * -100 = 84.65$$

$$EV(\text{STAY} \mid \text{testHI}) = 0.91 * -25 + 0.06 * 100 + 0.03 * -50 = -18.8$$

$$EV(\text{DECR} \mid \text{testHI}) = 0.91 * -50 + 0.06 * -25 + 0.03 * 100 = -43.5.$$

Still presuming that the test gave a result of testHI, we would choose the alternative with the maximum EV, so the maximum EV when the result is testHI is 84.65 ($EV_{\max}(\text{testHI}) = 84.65$). The same process is followed for the other test results and we end up with an EV_{\max} for each of them. This is the expected payoff of the decision after seeing each of the test results. In the foregoing analysis, we determined the probabilities of the various test results. Combining these with the EV_{\max} of each result gives the expected value *given* sample information ($EV|SI$):

$$EV|SI = \sum_{r=1}^R P(\text{result}_r) * EV_{\max}(\text{result}_r)$$

Using the probabilities of the test results, $P(\text{result})$, found in Table 1.4:

$$EV|SI = 0.293 * 84.65 + 0.373 * 73.89 + 0.333 * 86.25 = 81.17$$

The expected value of sample information (EVSI) is the difference of $EV|SI$ and EV_{prior} and measures will fall somewhere between the EV of the simple case and EVPI:

$$EVSI = EV|SI - EV_{\text{prior}} = 81.17 - 8.33 = 72.84.$$

In summary, expected value decision analysis uses the notion that a decision can be made over and over many times and that the best decision is the one with the greatest

average payoff. In a simple decision, using only the prior state probabilities, the decision-maker selects one alternative to maximize the expected value of the decision. With perfect information, the expected value of the decision is the probability-weighted sum of the best payoff for every state and the prior state probabilities. In the case of sample information, we use the sample to update the prior state probabilities to become the posterior state probabilities. The posteriors are used to find the maximum expected value of the decision for each possible inference based on the sample information. These are then combined into the EV|SI as the probability-weighted sum of the maximum expected values for each test result times the probabilities of obtaining those test results. The EV|SI is like a weighted average of separate decisions, each based on a certain result of the test.

Overview of Dissertation

This dissertation comprises three additional chapters emerging from a research initiative on behalf of the Vermont Fish and Wildlife Department to enhance data management and analytical capacity, to evaluate current practices, and to develop and apply new techniques in support of long-term management and conservation of wildlife. Each chapter is intended to stand alone, but they are linked by their intended application in improving decision-making for wildlife managers and conservation planners.

In Chapter 2, I compared the use of various population estimators in reference to different datasets to evaluate their statistical performance and the relationship between that performance and the dollar cost of the requisite data. I envisioned an estimation strategy as an estimator paired with a particular dataset. Using three common harvest-based estimators and five different datasets, I evaluated 8 alternative strategies. All of the

estimators used required age-at-harvest data and some were able to make use of additional data such as hunter-effort or marked animal recoveries. The 8 alternatives were compared on the basis of their bias and precision and on the expense required to collect the datasets. In this chapter, I introduce a new measure, the marginal value of data (MVD) to compare the statistical ‘return on investment’ obtained by investing in additional data for abundance estimation.

Chapter 3 is a value of information analysis based on the estimation strategies in chapter 2 when applied to a representative state-dependent harvest management decision problem. For this analysis, I computed the expected value of a decision made in ignorance, the expected value of perfect information (EVPI), and the expected value of sample information (EVSI) for each of the estimation strategies. EVPI indicates, in terms of the values placed on the decision outcomes, how much value is lost because we must choose an alternative (e.g. a management actions) when the true state of the system (e.g. population abundance) is uncertain. The EVSI is the gain in value when we can apply some sampling and estimation (e.g. abundance estimates) to reduce uncertainty about the system state.

Finally, in chapter 4, I develop a hybrid habitat modeling framework that embraces the need for deductive, expert-based models but couches them within a statistical framework. I used a novel approach, encoding expert opinion directly as a map and fitting a statistical model to that map, to facilitate rigorous revision of the HSI model through Bayesian methods analysis of an independent dataset as validation.

Taken together, these studies offer rigorous support to critical decisions facing wildlife managers today. I analyzed data of black bear in Vermont, but these methods are generally applicable to any harvested species and any region and can contribute to the decision-centric analytical toolkit of wildlife managers now and in the future.

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Table 1.1: Example Downing reconstruction for a single sex. The year “Final +1” is the hypothetical year constructed from average mortality counts. The mortality counts are on the left side of the table and the reconstructed abundances for each age-class and year are on the right side. The reconstructions are summed across age classes in column Rt. Abundances are not reconstructed for the final two years due to the gross inaccuracies resulting from reconstructing incomplete cohorts.

Year	Mortality Counts (C)				Adult Mortality rate (m)	Reconstructed abundances (R)				R _t
	0.5	1.5	2.5	3.5+		0.5	1.5	2.5	3.5+	
1	84	250	94	64	0.52	545	454	182	124	1305
2	155	285	134	97	0.66	493	461	204	148	1306
3	83	170	108	74	0.61	423	338	176	121	1058
4	71	180	104	71	0.62	476	340	168	115	1099
5	79	212	83	56	0.52	454	405	160	108	1127
6	77	200	121	81	0.63	452	375	193	129	1149
7	75	194	111	76	0.63	449	375	175	120	1119
8	78	179	97	58	0.54	493	374	181	108	1157
9	84	212	119	82	0.61	461	415	195	134	1206
10	90	195	122	77	0.60	421	377	203	128	1130
11	64	155	96	70	0.53	458	331	182	133	1104
12	108	211	109	92	0.62	295	394	176	149	
13	71	187	108	73	0.59	71	187	183	124	
Final+1			108	75	0.59			183	126	

Table 1.2: The (arbitrary) payoff values for a harvest management decision with three alternatives (INCR, STAY, DECR) and three possible system states (trueHI, trueAT, trueLO) describing the current population abundance relative to the target abundance. Choosing to increase harvest (INCR) has a high payoff value when the population is above the target (trueHI), but has negative payoff when the population is at or below the target because that alternative would cause the population to decline and move further away from the target.

Alternatives	States		
	trueHI	trueAT	trueLO
INCR	100	-50	-100
STAY	-25	100	-50
DECR	-50	-25	100

Table 1.3: Conditional probabilities of test results given true states, $P(\text{Result}|\text{State})$. Columns add to one. When the true state is above target (trueHI), the test result suggests the population is above target (testHI) 80% of the time, at target (testAT) 15% of the time, and below target (testLO) 5% of the time.

Results	States		
	trueHI	trueAT	trueLO
testHI	0.8	0.05	0.03
testAT	0.15	0.9	0.07
testLO	0.05	0.05	0.9

Table 1.4: A representation and worked example of computing joint probabilities of results and states, $P(\text{result} \& \text{state})$. The symbol “c12” indicates the conditional probability from the first row and second column of Table 10 and p1 is the prior probability of state 1 (trueHI). The sum of the rows is the probability of the test result (e.g. $P(\text{testHI})$). The prior probabilities for this example all equal 1/3. The posterior probability for each state given each result is computed by dividing each joint probability by the sum of its row.

Results	States			P(Result)
	trueHI	trueAT	trueLO	
testHI	c11*p1	c12*p2	c13*p3	sum(row1)
testAT	c21*p1	c22*p2	c23*p3	sum(row2)
testLO	c31*p1	c32*p2	c33*p3	sum(row3)

Results	States			P(Result)
	trueHI	trueAT	trueLO	
testHI	0.267	0.017	0.010	0.293
testAT	0.050	0.300	0.023	0.373
testLO	0.017	0.017	0.300	0.333

Table 1.5: Posterior probabilities of the states given the inferential results. Each cell in this table is the corresponding cell in Table 4b (right side), divided by the row totals ($P(\text{Result})$).

Results	States		
	trueHI	trueAT	trueLO
testHI	0.909	0.057	0.034
testAT	0.134	0.804	0.063
testLO	0.050	0.050	0.900

Chapter 2 The Best That Money Can Buy: Cost-Efficiency of Population Estimators

ABSTRACT Most wildlife management decisions are made in the face of uncertainty, often induced by limited data. Population estimates are integral to many management decisions, and they present choices about the analytical methods and the data to be used. Managers have many choices about how to develop the population metrics they need for management, but not all are necessarily worth the expense. In this paper, we introduce a marginal value metric to evaluate statistical gains in terms of dollars invested in data. We used simulated data on American black bear (*Ursus americanus*) to measure the performance of a suite of different combinations of estimators and datasets (“strategies”), including estimated costs of acquiring the datasets. The strategies were built around three alternative population estimation methods: population reconstruction (Downing 1980), a change-in-sex-ratio estimator (Paloheimo and Fraser 1981), and statistical population reconstruction and augmenting harvest data with hunter effort surveys and marked animal recoveries. Strategies were evaluated on their bias in representing abundance and annual growth rate and in their precision and bias relative to the cost of the data. Downing population reconstruction was the least biased in tracking growth trend, while statistical population reconstruction was best at estimating abundance. Our simple hunter effort survey contributed little to the performance of our estimators. This study demonstrates that complex methods and

expensive data are not necessarily an antidote to the fundamental uncertainty inherent in wildlife management.

KEY WORDS Abundance estimation, American black bear, cost-benefit, game species, harvest management, *Ursus americanus*.

State and provincial wildlife managers need to make management decisions and policy recommendations despite limited data and budgets. Because different analytical methods can result in different estimates for a given parameter, choice of analysis can lead to different management decisions, ultimately affecting wildlife populations.

Managers are tasked with setting harvest quotas to meet the objectives of sustaining wildlife populations and sustaining a harvest. If the harvest rate is too great, game populations can be suppressed to levels from which it may take many years to recover (Fryxell et al. 1988, Miller 1990, Taylor et al. 2008). This is a loss of value derived from both consumptive and non-consumptive interactions with wildlife by the human constituency of management agencies. On the other hand, if the harvest rate is too little, game populations may become overabundant and this may contribute to disease transmission (Gortazar et al. 2006), property damage and loss (West and Parkhurst 2002, Bissonette et al. 2008), human injury (Farrell et al. 1996, Hristienko and McDonald 2007, Bissonette et al. 2008), and ecological changes (Cote et al. 2004, McLaren et al. 2004, Cote 2005). These risks increase the need for more intensive and expensive management tactics (Fagerstone and Clay 1997, Hristienko and McDonald 2007, DeNicola and Williams 2008, Ransom et al. 2010).

To set harvest quotas that yield the target population size, unbiased and precise estimates of current population abundance are needed (hereafter, models used to estimate abundance from harvest data will be called “estimators”). Voluminous literature exists describing estimators developed to exploit information from harvested animals (Skalski et al. 2005). The estimators can be grouped according to their generalized approach. For instance, population reconstruction methods track the numbers of harvested individuals by age and sex through multiple years; an estimate of the population size at the beginning of each cohort can be obtained by tracing the harvest fate of the cohort through time. Alternatively, change in sex-ratio estimators (Paloheimo and Fraser 1981, Fraser et al. 1982, Fraser 1984) are commonly used when males and females experience different harvest pressure (Skalski et al. 2005). Finally, statistical population reconstruction methods combine auxiliary data (e.g., marked animal studies) to augment age-at-harvest data, enabling statistical estimation of survival, harvest, and abundance parameters (Gove et al. 2002, White and Lubow 2002, Skalski et al. 2005, Conn 2007, Skalski et al. 2007, Conn et al. 2008, Fieberg et al. 2010).

The manager’s choice of estimator must take into consideration data collection costs, particularly where additional data may make a viable choice of an otherwise unsuitable estimator. Examples of datasets that may accompany the age-at-harvest data include tag sales, the hunter participation rate (the proportion of hunters who actively hunt, given a tag was purchased), and the hours spent actively hunting per participant. Additionally, mark-recapture datasets permit estimation of harvest and survival rates.

From the manager’s perspective, the choice of which estimator is optimal likely depends on three critical objectives: minimizing the bias (the difference between the

estimated abundance and true abundance), maximizing precision (reducing the confidence interval of the estimate), and minimizing cost (the cost of the data needed for population estimation). New analytical methods are continually being developed (Skalski et al. 2005), presenting managers with an ever-increasing number of options for estimating the size or trend of a harvested population. Millspaugh et al. (2009) introduced the Coefficient of Error (CE), which summarizes the bias and precision of an estimator in a single metric. In this paper, we expand on their efforts and develop a Marginal Value of Data (MVD) metric, which measures the change in CE per unit cost of additional data.

We developed a simulation model of black bear population dynamics, harvest, and data collection under five scenarios of population growth, (2) estimated abundance of the simulated population with 10 alternative estimation strategies (estimator and dataset), (3) calculated the bias of each estimator with respect to abundance and population growth (λ), (4) calculated the Coefficient of Error (CE) for each estimator and scenario, and (5) estimated the Marginal Value of Data (MVD) for each estimator and scenario. Our approach can be applied to a wide variety of estimation methods to aid managers in selecting the most appropriate estimators, given budgetary constraints.

METHODS

This research was conducted by developing a population and harvest simulation model that can be parameterized to reflect a wide variety of game species and harvest regimes. Both models were functions within an R (R Core Team 2013) package called ‘AMharvest’, developed for the Vermont Fish and Wildlife Department, Vermont USA (Donovan et al. in prep). We used the function, popMod, to simulate population

dynamics through time. popMod is a discrete-time population model built around an annual cycle with non-overlapping periods within the annual cycle (**Error! Reference source not found.**). The census occurred in the autumn, followed by an autumn harvest season, a post-season survival period (winter-spring), an instantaneous breeding season (spring), and pre-hunting season survival (spring/summer). The model requires inputs for several key vital rates, including harvest rate, pre-breeding survival, birth rate (offspring per breeding female per year) birth sex ratio (the proportion of offspring that are males), and post-breeding survival.

For this study, we patterned the analysis after the American black bear (*Ursus americanus*) with 20 ages. Vital rates were made to fit generally the distributions documented by Beston (2011) in her meta-analysis of Black Bear demography, Bunnell and Tait (1985), and estimated harvest rates in Northern New England (F. Hammond, VT Dept. of Fish and Wildlife, and K. Gustafson, NH Fish and Game, pers. communication). Different simulation scenarios were facilitated by different parameterizations (“settings”) of age- and sex-specific vital rates (Table 2.1). Settings were chosen to produce population scenarios that were described as: stationary (finite rate of increase (λ) \approx 1.0), weak growth ($\lambda \approx$ 1.02), strong growth ($\lambda \approx$ 1.03), weak decline ($\lambda \approx$ 0.99), and strong decline ($\lambda \approx$ 0.96). These growth rates span the 95% credible interval of population growth rates identified for Black Bears in Eastern North America (Beston 2011).

popMod calls the function, annualHarvestMod, to simulate the harvest of animals on an annual basis. This function inputs the annual pre-harvest population census (from popMod) and annual harvest rate parameters for males and females, and outputs the total

number of harvested animals by age and sex. For simplicity, we assumed complete reporting and no errors in sexing or aging. The harvest rate was modeled as a logistic function with parameters for hunter effort, age, age^2 , density, and density^2 with the density covariate being abundance divided by 1000 (Table 2.1). We considered the harvest to be completely additive (and set the compensatory proportion of harvest to 0 in `annualHarvestMod`). Cubs were excluded from the harvest by design (to match reality) and therefore from all subsequent population estimates and comparisons.

Hunter effort was a key variable used to generate annual harvest rates for the alternative scenarios. Effort was represented in the model as thousands of hunter-days expended across an entire season. Conceptually, hunter effort arises from some number of hunters that purchase a tag or license, intending to hunt bears. Of these tag-holders, a subset will actively pursue bears that season and will do so for some number of days each. Hunter effort was simulated by random, normal deviates for thousands of tags purchased (mean = 4), participation rate (mean = 0.6), and average days hunted (mean = 5). These values are roughly similar to those seen in some jurisdictions with inexpensive tags. The product of these three random variables yielded the simulated value for thousands of hunter days, representing the total, annual effort. This formulation of effort allowed us to evaluate different proxies of effort (total number of tags sold vs. estimated hunter-days), with different strength of relationship with the simulated harvest rates and different costs associated with the requisite data.

Each of the five population growth scenarios was simulated under 2 different harvest scenarios, both of which included a binomial, stochastic harvest process, where the binomial trials were the number of animals of each age and sex available to be

harvested (the census population), and the probability of success was the harvest rate. First, the ‘constant-effort’ scenarios used mean levels of tag sales, participation, and days hunted for each year, with no annual variation in any of these components. Thus, total effort was tag sales * participation rate * hunter days. Second, the ‘variable-effort’ scenario allowed hunter effort covariates to vary from year to year by drawing annual values from Normal distributions with the stated means and standard deviations equal to 10% of each mean value. In either case, the total effort (days) was used as a covariate in generating annual harvest rates. Each setting was implemented for 100 iterations of 50 year simulations starting with previously determined stable age distributions. Initial population abundance was chosen so that total abundance in year 24 was approximately 6000 animals.

Datasets

In this study, we estimated the true pre-harvest population size with three commonly used estimators: Downing population reconstruction (Downing 1980), the change in sex ratio estimator of Paloheimo and Fraser ("Paloheimo-Fraser"; Paloheimo and Fraser 1981), and statistical population reconstruction ("SPR"; Skalski et al. 2005, Gast 2012), each of which required different datasets as inputs (Table 2.2). The fundamental dataset required by all three estimators was the counts of aged and sexed harvested animals ("harvest data"). The PF and SPR analysis required effort data, and the SPR analysis additionally required telemetry data for estimating harvest and survival rates.

In terms of effort data, the simulated tag sales were saved for every year in every simulation and made available to estimators as numbers known with certainty. The participation rate and hunter day surveys were conceived as having been distributed to known bear tag holders after the close of the harvest season. The data consisted of the response to the question: “How many days did you hunt for bears last (most recent) season?” We simulated 500 responses as a mixture of a Bernoulli distribution with a success probability representing the chance an individual hunter participates in an annual bear season (i.e., probability of participation = 0.6) and a Poisson distribution with a mean representing the mean days afield for participating (active) hunters (5).

In terms of telemetry data, we simulated two, alternative tag-recovery datasets with varying intensities, with average values of 12 (spr12) versus 25 (spr25) animals captured annually. Both sexes were deemed equally available to capture, survived at the same rates as the larger, simulated population, and were re-sighted without error.

Representative monetary costs were assigned to the different datasets in order to assess information quality relative to expense. The cost functions are merely representative and not meant to be rigorous estimates. They capture the relative magnitudes of costs among projects of this size. Harvest data and tag sales were considered to have costs of zero because the data are collected regardless of estimator type. Costs were nominally considered in units of \$1,000. The hunter survey was assigned a cost of 1 on the assumption that it could be accomplished largely within the existing efforts of state biologists (e.g. use questionnaires during check-station duties) and the marked animal datasets were assigned 70 and 100 for the small and large datasets, respectively. Marked animal dataset costs were estimated roughly using budgets

for similar projects. SPR strategies that estimated hunter-days (spr12_hd and spr25_hd) carried costs for marked data and the survey (71 and 101).

Estimators

Given the age-at-harvest dataset, the effort dataset, and the tag-recovery datasets as potential inputs, we then estimated the true population size (pre-harvest) for each population growth scenario (stationary, weak growth, strong growth, weak decline, and strong decline), and harvest scenario ('constant-effort' and 'variable-effort') with each of the three estimation methods. These estimator functions are named `downingEst` (Downing Population Reconstruction), `pfEst` (Paloheimo and Fraser), and `bsprEst` (Bayesian Statistical Population Reconstruction), respectively in the `AMharvest` package (Donovan et al. in prep).

The Downing method of estimating abundance from harvest data is a well-known population reconstruction method (Downing 1980); its sole input is the age-at-harvest data (Table 2.2). The Downing method has been subject to several performance assessments (Davis et al. 2007, Fieberg et al. 2010) and is known to be a negatively-biased abundance estimator that, when assumptions are satisfied, effectively tracks population trend. This method does not estimate vital or harvest rates (except a weak proxy of adult mortality) but reconstructs the pre-hunt population by backward-addition of known mortality and a minimal assumption of unaccounted-for mortality (Downing 1980). Downing reconstruction performs best with cohorts that are fully represented in the harvest data. The reconstruction is robust to the pooling of adult age classes, and the

practice is recommended (Davis et al. 2007). We pooled our data into 6 classes, 5 for animals of ages 1 through 5 and a sixth class for animals of age 6 or greater.

The Paloheimo-Fraser (PF) method estimates sex-specific harvest rates according to the assumption that one sex is more vulnerable to harvest (Paloheimo and Fraser, 1981). Differential vulnerability causes harvest ratios to be skewed toward the more vulnerable sex in younger age classes but to reverse in older age classes as the more vulnerable sex is depleted from the population. Male black bears, among others, are known to be more vulnerable to harvest than females. Fraser (1984) found that one could approximate the composite (i.e. average across sexes) harvest rate as the reciprocal of the age at which female:male harvest ratio exceeds one (e.g. females first predominate as 10 year-olds implies composite harvest rate of 0.10). Paloheimo and Fraser (1981) and Fraser et al (1982) exploited this relationship to estimate sex-specific harvest rates and use them to reconstruct the population abundance as the harvest count divided by the harvest rate. We estimated harvest rate for males and females as a function of annual hunting effort; thus the main inputs for this method were the age-at-harvest data and annual effort data.

For our Paloheimo-Fraser estimator, we parameterized harvest rate as a Poisson catch (Paloheimo and Fraser 1981, Seber 1982):

$$1 - \exp(-v_{sex} * effort_i),$$

with sex-specific vulnerability parameters (v) that depict the per-unit of effort vulnerability to harvest of each sex. When combined with effort from each year (i), this results in annually varying harvest rates. For the sake of estimation, the sex-specific

vulnerabilities comprise 2 independent parameters, p and u , such that $v_{female} = p-u$ and $v_{male} = p+u$. The parameters p and u are then estimated by weighted non-linear least-squares regression of the log harvest ratio over age (Paloheimo and Fraser 1981). To reduce inter-annual random variation in harvest counts, we used a 3-year rolling average of current and 2 prior years' harvest data for analysis. This meant that the result of analysis in year Y was an estimate of abundance in year Y-1, and this adjustment was made for all comparisons and visualizations.

Harris and Metzgar (1987) analyzed of the performance of the Paloheimo-Fraser method under violations of the method's key assumptions: Both sexes equally abundant in the age class prior to the youngest age class in the harvest (or that sex ratios are empirically known); no systematic changes in sex-specific vulnerability occur with increasing age; and differential vulnerability to harvest as the only factor influencing sex ratios. They found the models sensitive to violations of each of the assumptions and strongly cautioned users of these methods. They also noted that even under appropriate conditions, harvest rate estimates can be substantially more variable than the true rates. This estimator requires only harvest and effort data, so it is an attractive option for many managers and we wished to see how it compared to other options.

The final estimator we evaluated required age-at-harvest data plus ancillary data such as mark-recapture data that is used to estimate both harvest rate (including effort) and natural mortality rate (Table 2.2). Statistical population reconstruction (SPR) is a term applied to a class of population estimators that are similar to classic population reconstruction techniques, but use auxiliary data to support estimation of nuisance parameters that cannot be estimated from harvest data alone (Gove et al. 2002, Skalski et

al. 2007, Skalski et al. 2011, Gast et al. 2013). SPR is not *an* estimator, but rather a type of model for estimation from multiple sources of data and different parameterizations are possible. The fundamental feature is that multiple sources of data are exploited jointly for parameter estimation. Whereas the Downing method relies on a simplistic estimate of adult mortality, derived entirely from the harvest data, SPR affords the analyst the opportunity to estimate mortality from both the harvest and auxiliary data such as marked animal recoveries. The statistical estimation inherent in SPR allows quantification of uncertainty, a glaring absence from traditional reconstruction methods (e.g. Downing).

Statistical population reconstruction operates on harvest data within cohorts in a manner similar to traditional reconstruction methods, but uses maximum likelihood methods to find the most likely parameter estimates for harvest rates and natural survival rates that would generate the observed harvest data and telemetry data. Gast (2012, 2013) assessed the statistical performance of various forms of SPR, including some with and without random effects and recruitment functions. The best-performer in his study was one that estimated only harvest vulnerability and survival (Gast et al. 2013). This estimator formulates the likelihood of the harvest and survival rates within a cohort are modeled as conditional upon the total harvest of that cohort (p.1261, Gast et al. 2013). The estimated harvest and survival rates can then be used to estimate abundance of each cohort from the harvest counts.

We used Gast's conditional SPR formula (fixed effects only) with harvest rate parameterized as a Poisson catch with per-effort vulnerability (v), and natural survival rate parameterized as a probability (i.e., identity link). Although other options are

possible, given our focus on sparse data, we estimated a single annual natural survival rate across all years of the auxiliary dataset. We used this form, with only fixed effects, as our basic SPR estimator, which we formulated as a Bayesian model with joint multinomial likelihoods for harvest and survival. We used uniform prior distributions for survival, harvest vulnerability, and mean days hunted and fit the SPR models with WinBUGS (Lunn et al. 2000) from within R using the package R2WinBUGS (Sturtz et al. 2005).

The three estimators and various datasets were compiled into 8 different population estimation “strategies” consisting of each method matched to one or more suitable datasets (Table 2.2). The Downing method was performed using only harvest data (strategy = “dnull”). The Paloheimo-Fraser method was used with 1) only harvest data and an assumed, constant level of effort applied across all years (“pfnnull”), 2) harvest data and tag sales as a proxy of effort (“pftags”), and 3) harvest data and hunter-days calculated as tag sales times mean days hunted per hunter. The mean days hunted was estimated as a simple average of the responses to the simulated hunter effort survey. Residual analysis was performed on select iterations of the Paloheimo-Fraser method. No evidence suggesting systematic lack of model fit to the data was observed. The SPR strategies all used the same SPR model but the data differed in 2 dimensions. First, SPR strategies used either the smaller (spr12) or larger (spr25) marked animal datasets, and second, they used either tag sales as the index of effort (tags) or hunter-days as the measure of effort (hd; Table 2.2). In the latter case, the SPR models estimated mean days hunted across all individuals in the effort survey and the product of mean days and tag sales was the estimate of hunter-days. Following the model-fitting suggestions of Skalski

et al (2012), we calculated Anscombe residuals and plotted them by age and by year for select instances of our SPR estimations. The residuals gave no indication of systematic lack of fit to our data. We did not attempt to test sensitivity to annual data by dropping some years from analysis. This type of sensitivity is likely high and unavoidable in the short duration studies we simulated.

All population estimators were run with custom computer code and were tested prior to use. Downing and PF model code successfully reproduced the results from the primary literature sources for both estimators. SPR code faithfully estimated simulation inputs for small simulation datasets created for model-testing.

For each of the five population growth scenarios, comparisons among the eight alternative strategies were made across the 25th to 45th years of the simulations. Given our use of 6 age classes for the Downing reconstruction, the most recent 5 years (years 45-50) could not give reasonable reconstruction estimates due to incomplete cohorts in the harvest data and were dropped from the comparisons. The Paloheimo-Fraser methods that do not assume a constant annual effort (pftags, pfhd), require estimates of the cumulative hunting effort to which the oldest animals have been exposed. As 20 years was our terminal age, this required 20 years of past effort data to parameterize the model so the Paloheimo-Fraser method could only be applied to our simulated data starting in year 21. Our marked animal studies were simulated for only 6 years so SPR estimates are only available for years 25-30. Years 31-45 are therefore missing for SPR and performance of SPR strategies is based on only 6 years of data per simulation.

Coefficient of Error

We estimated the performance of each estimator on simulated harvest datasets in terms of bias and precision. We measured the relative bias in abundance estimates by taking individual annual abundance estimates, subtracting the true abundance and then dividing by the true abundance ($[\widehat{N} - N]/N$), and then finding the median value across the focal years (25-45) and all simulations for a given setting. As an index of the dispersion across individual years, we also calculated the standard deviation of all bias measures per setting. We calculated median percent bias for growth rate estimates in the same manner. First we calculated the annual growth rate ($\lambda_t = N_{t+1} / N_t$) for true and estimated abundances and took the median and standard deviation of the focal years and all simulations for each setting.

We also calculated a single summary of bias and precision for abundance estimates using the Millspaugh et al (2009) Coefficient of Error (CE), expressed as a percentage:

$$CE = \frac{\sqrt{\widehat{MSE}}}{\left(\frac{\sum_{i=1}^n \sum_{j=1}^y N_{ij}}{ny}\right)}, \text{ where}$$

$$\widehat{MSE} = \frac{1}{n} \sum_{i=1}^n \left[\frac{\sum_{j=1}^y (\widehat{N}_{ij} - N_{ij})^2}{(y-1)} \right],$$

y is the number of years being compared ($y = 21$), n is the number of simulations ($n = 100$), N_{ij} is the true population for simulation i and year j , and \widehat{N}_{ij} is the associated abundance estimate.

Marginal Value of Data

We compared the marginal value of investment in data for a given strategy (estimator plus datasets) by first averaging the CEs for each strategy across all five simulation settings (strong decline, weak decline, stationary, weak growth, and strong growth). The lowest mean CE of the no-cost strategies (dnull, pfnnull, pftags) became the baseline for comparison. We then computed the gross change in CE (as a percentage) relative to the baseline and divided it by the cost of the data required by that strategy to the marginal value of data (MVD):

$$MVD = \left[\frac{(\overline{CE}_i - \overline{CE}_{baseline})}{\overline{CE}_{baseline}} \right] / Cost_i$$

The MVD is the percentage change in CE per unit investment in additional data. Because the intent of the manager would be to reduce CE through investment, desirability of MVD is inversely proportional to its numeric value. An MVD of -10% is better than -5%, and so on. A positive MVD indicates that a one unit increase in cost results in a positive change, an *increase*, in CE.

MVD measures how much you can change the CE of your estimates by buying new data, but on a per-unit cost basis. Suppose you currently analyze only harvest data so there is no additional data cost and your method has a CE of 0.40. By investing \$50,000 dollars in additional data, you could reduce the CE to 0.25. That is a -37.5% change in CE ($(25-40)/40 = -0.375$). Taking costs in units of \$1,000, the MVD would be -0.75% ($-37.5/50$), meaning each \$1,000 invested in data reduces the CE by 0.75%. Perhaps a third alternative cost \$100,000 and delivered a gross change in CE of -50%. This strategy

would have an MVD of only -0.5% per \$1000 invested in data. The absolute improvement is greater, but the marginal improvement is less.

RESULTS

The growth rates for the five base population simulations were approximately 0.96 (strong decline), 0.99 (weak decline), 1.0 (stationary), 1.02 (weak increase), and 1.03 (strong increase; Figure 2.2, Table 2.1). Effort for all years of variable-effort simulations ranged between 2.27 and 5.8 thousand tags (mean = 4, sd = 0.4) and between 5 and 24 thousand hunter-days (mean = 12, sd = 2). The correlation between tags and hunter-days was 0.58. Nominal harvest rates (calculated at the intercept, without covariates) varied between 0.05 and 0.08 for females and 0.08 and 0.13 for males. Positive age effects result in pre-breeding survival between .90 and 1.0 for adults, and post-breeding survival rates between 0.80 and 0.85 for males and 0.85 and 0.88 for females. Annual birth rates ranged between 1.03 and 1.22 cubs per breeding-age female per year.

Abundance Bias

Empirical distributions of bias are shown in Figure 2.3 and summarized in Table 2.3. The Downing estimator had median relative bias ranging from -33% to -49% across all simulations (constant- and variable-effort; “dnull”). Distribution of bias across settings was consistent between constant-effort and variable-effort harvest conditions.

The Paloheimo-Fraser strategies were consistently negatively-biased across all simulations with median values from -20% to -39% (Figure 2.3; “pfnnull”, “pftags”, “pfhd”). Regardless of whether effort was constant or variable, there was little difference

in bias among the various Paloheimo-Fraser strategies. The method that incorporated hunter effort surveys to estimate hunter-days (pfhd) was essentially as biased as the method assuming constant effort (pfnnull), even when the simulated data was generated using annually variable hunter effort.

Across all simulation settings, the SPR strategies were the least biased of all strategies, and their bias tended to be positive. The SPR strategies were also the most volatile. Median bias for all SPR strategies fell between -6% and 26%. Greater bias was seen with smaller datasets and variable-effort simulation settings. Median bias was between -5% and 5% for the larger dataset strategies and between 5% and 26% for the smaller datasets. Performance of the tags-only strategies relative to the hunter-days strategies was mixed. The greatest bias was seen in the small sample, hunter-days strategy (spr12_hd), but for many simulation settings, the tags and hunter-days versions performed nearly identically.

Growth Rate Bias

Bias in growth rate estimation for all three estimators was two orders of magnitude lower than that for abundance estimation (Figure 2.4; Table 2.4). Median relative bias for growth rate estimated from the Downing method was small and stable across all simulation settings, ranging from -0.19% to 0.35% for constant-effort harvest settings and from -0.18% and 0.35% for variable-effort harvest settings. Bias was least for the stationary population settings and increased as the true growth rate moved away from 1, but these differences were negligible.

The Paloheimo-Fraser strategies performed well, but with more variability than Downing. Median relative bias ranged from -0.46% to 0.51% across all simulations. The greatest median bias was 0.51% for pfnnull (weak growth scenario, variable-effort setting), -0.46% for pftags (weak decline, variable-effort), and 0.29% for pfhd (weak decline, constant-effort). The least bias for the 3 strategies were -0.02% for both pfnnull and pftags (stationary, variable-effort), and 0.06% for pfhd (strong decline, constant-effort).

The SPR strategies generated slightly more biased growth rate estimates than the Downing and Paloheimo-Fraser strategies. Median bias varied between -1.27% and 0.75% across all strategies for the constant-effort settings. For the variable-effort settings, median bias of all strategies ranged between -0.71% and 2.16%. Bias was more variable (wider ranges) for strategies using hunter survey data (suffix = “hd”) to estimate hunter-days than for those using tags as the index of effort (suffix = “tags”).

Coefficient of Error

The Coefficient of Error (CE) summarizes bias and precision in a single value (Millspaugh et al. 2009), such that a perfect estimator would have a CE of 0. Downing reconstruction had the greatest coefficient of error of abundance estimates (mean across all settings = 0.43, range = 0.15; Figure 2.5, Table 2.5). The Downing CEs were essentially identical across constant-effort and variable-effort harvest settings. The Paloheimo-Fraser strategies had slightly better (lower) but more variable performance than the Downing. The SPR strategies had the lowest CEs overall. Among the SPR strategies, CEs were generally lower and more consistent for 1) tags vs hunter-days, 2) constant-effort vs. variable-effort, and 3) larger vs. smaller datasets.

The coefficient of error values of the growth rate estimates were substantially lower than the CEs of the abundance estimates. The CE for Downing growth rate estimates averaged 0.01 (Figure 2.6, Table 2.6), the lowest CE of all strategies (and hence the best). The Paloheimo-Fraser strategies were very consistent with one another and had the greatest CEs and ranges of all strategies. The SPR strategies had mean CE values between 0.03 and 0.04 for constant-effort settings and between 0.06 and 0.08 for variable-effort setting.

Marginal Value of Data

The baseline strategy for abundance estimation was the Paloheimo-Fraser strategy using tags (pftags) and the baseline for growth rate was Downing (dnull). These were the two best, no-cost performers in terms of CE for abundance and growth rate estimation, respectively. Other strategies of abundance estimation greatly reduced the CE from the baseline of pftags. SPR strategies were able to reduce the CE by as much as 85% overall (Table 2.7). The smaller sample SPR strategies had lesser gross reduction in CE (from the baseline) than the larger dataset strategies, but their MVDs were comparable. Adding marked animals to the study improved performance, but on a per-dollar basis, they delivered slightly less bang-for-the-buck than the smaller dataset. For every additional unit investment in data, our SPR strategies reduced the CE by around 0.8% (Table 2.7). None of the MVD values for growth rate estimation were negative, which means that none of the investment in data was able to improve upon the Downing (dnull) growth rate estimates.

DISCUSSION

Population estimators are typically evaluated on the basis of their statistical performance, either under ideal conditions, or with respect to violations of assumptions. These are important aspects of understanding wildlife management tools, but they do not address all relevant aspects of the decision of which tools to use. The SPR strategies were the best for estimating abundance, but the real question for a manager is whether the performance justifies the cost.

The estimation strategies we examined were combinations of population estimators and datasets representing different costs and amounts of information. We used the MVD statistic as a means of identifying the per-dollar performance improvement gained by “buying” a better dataset. By comparing the estimation strategies to a no-cost base case, we can evaluate how much improvement is to be gained from investment in additional data. What we see is that better estimation strategies may not always offer commensurate reward to the dollars invested. The best method of estimating growth rate requires no auxiliary data. Any dollars spent pursuing better estimates did not result in improvement. Better abundance estimates can be achieved with better data. Hunter effort survey contributed little improvement to abundance estimates, but auxiliary survival data made a big difference and may be worth the investment.

Our focus was strictly on the question of measuring the benefit of additional data on population monitoring information for managers of harvested species. The MVD comparison ignores knowledge “thresholds”. If there is some information that is critical to management that can only be obtained through a large investment, this is not reflected in the MVD which is measuring on the reduction in CE of population abundance or

growth rate estimates. Likewise, we did not account for ancillary scientific and other benefits to be gained from engaging in more intensive data-collection, nor did we include cost-sharing among partner organizations. These considerations can and should also be included in a responsible cost-based evaluation.

The costs we used were used as rough, albeit robust, guides to required investment in various datasets. Our intent was to examine the cost of gathering data relative to the results of analyzing the additional information.

Examination of MVD comparisons across a range of reasonable data costs achieves results consistent with those reported here (unpublished analysis) as the uncertainty in cost of a given strategy is less than the differences among the alternative strategies. The costs of generating marked animals datasets are considerable, so there will always tend to be a gap between the cost of these and other data such as surveying a sample of licensed hunters. Although researchers are not limited to large, discrete steps in their intended sample sizes (e.g., 12 or 25 animals), a small difference such as adding 2 more animals, is not likely to offer improved inference. Some non-trivial “step” up in cost is to be expected if one intended to undertake a study that had a substantially better chance of delivering reliable inference than some other, smaller option.

Plausible sample sizes for such studies will depend on the species of interest and the location of application. Bears are difficult to capture and collar in large numbers. A technique of using chemical traces in broadly-distributed bait is used for marking bears in Minnesota (Garshelis and Visser 1997), but attempt to reproduce this technique in Vermont have failed (F. Hammond, pers. comm.). Other species may be more amenable

to capture in larger numbers (e.g. deer) and lower cost, so cost-effectiveness of methods requiring auxiliary data needs to be evaluated on a case-by-case basis. We simulated a particular kind of auxiliary data, an expensive one, and it is important to remember that SPR need not rely on such datasets for auxiliary information. Other options are available depending on the species of interest, but typically, adequate auxiliary data will be intensive, and therefore require non-trivial amounts of time and money to collect. The SPR strategies we examined differed by the size of the dataset (animals marked) and this will always result in substantive differences in cost. Of course, once an initial investment in marking is made, small additional amounts can be invested to increase the size and value of the dataset incrementally. We also simulated rather optimistic datasets with very high capture rates, no damage to the animals, and no malfunction in equipment. In practice, such studies are typically less productive than planned, driving up their cost relative to the information they can deliver.

The amount of bias we found in the Downing reconstruction was consistent with other published analyses of this reconstruction method. Davis et al (2007) corroborated Downing's assertion that the magnitude of negative bias will be proportional to the amount of mortality that is absent from the data. Downing's original description of the technique used data on an intensively-studied deer herd living within a 137 km² study area. These deer were the subjects of well-regulated hunting with persistent and intensive monitoring of both deer and hunters (Downing 1980). Downing then takes great pains to account for all sources of mortality and bases his reconstruction on total mortality, not just harvest. Our simulation conditions included natural survival rates were as low as 80% for some age-, sex-classes. We also parameterized the simulated harvest rates with a

quadratic effect of age such that harvest rates peak for sub-adults and animals just entering adult-hood, a pattern of high harvest on mobile, inexperienced animals that is seen in the field. The combination of natural survival and harvest rates, consistent with actual populations, is the likely cause of bias in our Downing analysis.

The results of the Paloheimo-Fraser method were also strongly negatively-biased. Harris and Metzgar (1987), in their performance analysis of the PF method noted that this method suffers the same fundamental weakness as the Downing reconstruction. When using only harvest data and estimating harvest rates, non-harvest mortality is ignored and therefore the estimation of abundance is negatively-biased. Bias can also result from differential non-harvest mortality between sexes, a phenomenon known to occur in black bears and present in our simulations. Also, bear harvest data typically begin with 1.5 year-old animals (cubs are rarely harvested) but it assumes that the population sex ratio is 1:1 at this time. Differential mortality between males and females from birth to 1.5 years can also induce bias. Finally, the Paloheimo-Fraser method is also rather volatile. Our results are consistent with those of Harris and Metzgar (1987) who found that the coefficient of variation (CV) of estimated harvest rates can be an order of magnitude greater than the CV of the actual rates.

In our study, the inclusion of hunter survey data did not improve model performance, despite the fact that others have shown variations in the number of hunters afield explaining a large part of the year to year variation in bear harvests (Noyce and Garshelis 1997). By leaving the survey data out and using only tags, we reduced the total uncertainty and improved model performance. Two factors influence the degree to which hunter effort data will be helpful in harvest estimation: the strength of the effort effect on

annual harvest rates and the inter-annual variability in effort. Other covariates of vulnerability to harvest, such as food availability (Noyce and Garshelis 1997) could also be helpful in estimating bear vulnerability, but they would need to meet the same conditions to constitute an improvement. Ultimately, variation in hunter effort may introduce noise into the analysis such that using a simple proxy (e.g. tag sales) can actually be preferable, even optimal, relative to other measures.

We examined the efficacy of small datasets for implementing SPR and found them to be potentially adequate. Not surprisingly, larger sample size for the SPR auxiliary data improved model performance, but at a cost. The SPR methods have very broad credible intervals for bias in abundance and growth rates and this could be due to small sample sizes. We saw little improvement in bias reduction when auxiliary datasets were simulated for up to 75 new captures annually (unpublished analysis), but precision of the estimates did improve. As stated above, our auxiliary datasets unrealistic in terms of high capture rates and no “losses” (equipment failure, etc.), so in practice, the SPR performance seen here may only be achievable with even greater expense and effort. Larger datasets could support age- or class-specific analysis that might better account for the harvest and survival processes and further reduce bias.

Estimator performance was markedly different depending on whether the intent was abundance estimation or tracking growth rates. The latter task is apparently easier and can be done for no additional investment in data beyond aged and sexed harvest data. Although all strategies were effective at tracking growth rates, the volatility of the Paloheimo-Fraser method suggests caution in using this approach blindly. Fieberg, et al (2010) found SPR-type models superior to Downing. Their study found similar degrees

of error for Downing as we did (e.g. $MSE = 0.009$) while their integrated models performed much better (e.g. $MSE = 0.00005$), but the practical contribution of such improvement to management is debatable. Given our focus on small-sample scenarios, we found the Downing method to be superior to the other strategies.

MANAGEMENT IMPLICATIONS

Our research shows that for game species management, improvements in abundance estimation require investment in improved data, while excellent growth rate estimates can be had for no investment beyond the collection of harvest data. Simple methods for basic data are available, but they require more stringent assumptions than more sophisticated methods that require more intensive data. Ideally, funds are invested in validating these assumptions, but often, that is not the case.

SPR can be an excellent tool under the right conditions and can be cost-effective relative to launching an intensive population estimation study utilizing capture-recapture methodologies. SPR is relatively free from dubious assumptions and performs well at estimating abundance and taking advantage of formerly disparate datasets. However, where sufficient data do not already exist, the cost of obtaining it likely outweighs the value to the manager in terms of harvest and population management decision-making. Skalski et al (p. 1315, 2007) point out that the needs of SPR can focus the objectives of intensive population studies. While this is undoubtedly true, the ultimate impact of the information and analyses should be considered relative to the decisions facing wildlife managers.

The MVD statistic can provide a rough guide for incremental investments as well as the distinct, discrete options we present here. What makes the MVD analysis work is the comparison of the costs of data to a clearly articulated benefit or set of benefits, in this case, estimation bias and precision. Given those objectives, a cost-benefit comparison can be made and the range of options compared. Again, our results are conditioned on our framing of the issue as one of monitoring a harvested population (Chapter 3 connects these objectives to the ultimate objectives of a harvest manager). Other objectives could lead to other conclusions, but our results suggest that the marginal benefit of an investment in data could be an important consideration prior to allocating resources.

The critical deciding factor in our comparison of these estimation strategies is the importance of abundance estimate. In choosing a population analysis strategy, managers must identify their values relative to estimating abundance and growth rate. There is no one-size fits all “answer” to the challenges of population management, but where budgets are limiting, management strategy should take a hard look at not just information that would be good to know, but information that would change the decisions that are made (for more on this, see Chapter 3). When the upper limits of the wildlife population are defined primarily by human/social drivers, rather than ecological, the task of providing precise and accurate estimates of abundance may be unnecessary year-to-year as management will typically be tied to detection of differences in abundance (rates of change) rather than attempts to meet some numerical target, per se.

Consistent, though biased, abundance estimates and precise estimates of growth rate may be adequate in many cases, but such methods do expose managed populations to some risk. A declining population could still have high, stable harvests which could lead

to misdiagnosis of the true population state. For that reason, some checks on the absolute abundance of the population are in order, most likely on a periodic, basis. Periodic investment in intensive data designed to test assumptions that might also be exploited for 'benchmark' abundance estimates within a regular program of low-cost annual trend-tracking.

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FIGURE LEGEND

Figure 2.1: Annual cycle of events in the simulated population.

Figure 2.2: Simulated population trajectories across years 20-50

Figure 2.3: Empirical bias in abundance estimation (gray zone is 95% credible interval).

Figure 2.4: Empirical bias in growth rate estimation (gray zone is 95% credible interval).

Figure 2.5: Distribution of CE values for abundance estimates.

Figure 2.6: Distributions of CE values for growth rate estimates.

Table 2.1: Parameter values used for simulating vital and harvest rates. Sample rates, calculated at the intercept, are displayed. Birth sex ratio was modeled as 1:1 for all simulation scenarios.

Simulation sub-model		Simulation scenarios				
		strong decline	weak decline	stationary	weak increase	strong increase
Female Harvest rate (logistic)	value at intercept:	0.08	0.06	0.05	0.05	0.05
	intercept	-2.4	-2.7	-2.9	-3	-3
	age	0.02	0.02	0.02	0.02	0.02
	age squared	-0.002	-0.002	-0.002	-0.002	-0.002
	density		0.01		0.01	0.01
	effort	0.035	0.035	0.035	0.035	0.035
Male Harvest rate (logistic)	value at intercept:	0.13	0.10	0.10	0.08	0.12
	intercept	-1.9	-2.2	-2.2	-2.5	-2
	age	0.02	0.02	0.02	0.02	0.02
	age squared	-0.002	-0.002	-0.002	-0.002	-0.002
	density		0.01		0.01	0.01
	effort	0.035	0.035	0.035	0.035	0.035
Female Post-breeding survival (logistic)	value at intercept:	0.85	0.88	0.88	0.88	0.88
	intercept	1.7	2	2	2	2
	age	0.2	0.2	0.2	0.2	0.2
	age squared	-0.005	-0.006	-0.005	-0.006	-0.006
	density		-0.005	-0.05	-0.005	-0.005
Male Post-breeding survival (logistic)	value at intercept:	0.80	0.85	0.85	0.85	0.85
	intercept	1.4	1.7	1.7	1.7	1.7
	age	0.2	0.2	0.2	0.2	0.2
	age squared	-0.005	-0.006	-0.005	-0.006	-0.006
	density		-0.005	-0.05	-0.005	-0.005
Birth rate (cubs/female/year) (Poisson)	value at intercept:	1.03	1.16	1.22	1.22	1.08
	intercept	0.03	0.15	0.2	0.2	0.08
	density		-0.008	-0.008		
	density squared	-0.001	-0.005	-0.005		-0.001

Table 2.2: The 8 alternative estimation strategies. As one moves downward through the table, the strategies include increasing sophistication of estimator and intensity of data. The ‘pfnnull’ strategy assumes constant annual effort, ‘pftags’ uses tag sales as the index of effort, and ‘pfhd’ uses hunter-days, calculated as the product of tag sales and the mean days hunted as reported on hunter surveys. The statistical population reconstructions differ in 2 dimensions. First, they use either the smaller or larger marked animal datasets, and second, they use either tag sales as the index of effort, or mean days hunted were estimated jointly with other parameters and used with tag sales to calculate hunter-days as the index of effort.

Name	Estimator	Harvest data	Tag Sales	Hunter Effort	Marked Animal Data	
					Small (12)	Large (25)
dnull	Downing Reconstruction	x				
pfnnull	Paloheimo-Fraser	x				
pftags	Paloheimo-Fraser	x	x			
pfhd	Paloheimo-Fraser	x	x	x		
spr12_tags	Statistical Population Reconstruction	x	x		x	
spr25_tags	Statistical Population Reconstruction	x	x			x
spr12_hd	Statistical Population Reconstruction	x	x	x	x	
spr25_hd	Statistical Population Reconstruction	x	x	x		x

Table 2.3: Median relative bias for abundance estimates.

	Constant Effort					Variable Effort				
	strong decline	weak decline	stationary	weak growth	strong growth	strong decline	weak decline	stationary	weak growth	strong growth
dnull	-0.334	-0.422	-0.448	-0.489	-0.394	-0.331	-0.423	-0.446	-0.489	-0.394
pfnnull	-0.384	-0.348	-0.333	-0.374	-0.197	-0.383	-0.345	-0.335	-0.368	-0.196
pftags	-0.384	-0.348	-0.333	-0.374	-0.195	-0.384	-0.345	-0.333	-0.369	-0.196
pfhd	-0.385	-0.349	-0.332	-0.372	-0.194	-0.383	-0.342	-0.332	-0.371	-0.194
spr12_tags	0.107	0.043	0.079	0.108	0.102	0.119	0.093	0.155	0.018	0.035
spr25_tags	-0.036	-0.036	0.021	-0.048	0.006	-0.020	-0.014	0.002	-0.042	-0.019
spr12_hd	0.096	0.050	0.087	0.104	0.103	0.095	0.093	0.264	0.056	0.029
spr25_hd	-0.031	-0.032	0.011	-0.056	0.023	-0.028	0.023	0.001	0.005	-0.027

Table 2.4: Median relative bias of growth rate estimates.

	Constant Effort					Variable Effort				
	strong decline	weak decline	stationary	weak growth	strong growth	strong decline	weak decline	stationary	weak growth	strong growth
dnull	0.003	0.001	0.000	-0.002	-0.002	0.004	0.001	0.000	-0.001	-0.002
pfnnull	0.001	0.003	0.002	-0.002	0.001	-0.001	-0.004	0.000	0.005	0.002
pftags	0.001	0.003	0.002	-0.002	0.001	-0.001	-0.005	0.000	0.003	0.002
pfhd	0.001	0.003	0.002	-0.002	0.001	-0.002	-0.002	-0.001	0.002	0.002
spr12_tags	-0.003	-0.002	0.008	-0.002	0.001	0.003	0.001	0.003	0.001	0.010
spr25_tags	-0.004	-0.002	0.004	0.002	0.001	0.005	0.001	0.001	-0.002	0.010
spr12_hd	-0.004	-0.012	0.004	-0.005	-0.002	0.004	0.021	-0.006	0.010	0.022
spr25_hd	-0.004	-0.013	0.006	-0.002	-0.003	0.000	0.007	0.001	-0.008	0.016

Table 2.5: Coefficients of error (CE) of abundance estimates.

	Constant Effort					Variable Effort				
	strong decline	weak decline	stationary	weak growth	strong growth	strong decline	weak decline	stationary	weak growth	strong growth
dnull	0.35	0.43	0.46	0.51	0.41	0.35	0.43	0.46	0.51	0.41
pfnnull	0.42	0.37	0.35	0.39	0.21	0.41	0.37	0.35	0.39	0.21
pftags	0.42	0.37	0.35	0.39	0.21	0.41	0.36	0.34	0.39	0.21
pfhd	0.41	0.37	0.34	0.39	0.21	0.41	0.36	0.34	0.39	0.21
spr12_tags	0.14	0.11	0.13	0.21	0.10	0.31	0.15	0.21	0.14	0.13
spr25_tags	0.08	0.08	0.06	0.05	0.06	0.09	0.09	0.10	0.08	0.09
spr12_hd	0.15	0.11	0.14	0.21	0.10	0.45	0.19	0.27	0.14	0.19
spr25_hd	0.09	0.09	0.07	0.06	0.07	0.13	0.12	0.13	0.10	0.08

Table 2.6: Coefficients of error (CE) of growth rate estimates.

	Constant Effort					Variable Effort				
	strong decline	weak decline	stationary	weak growth	strong growth	strong decline	weak decline	stationary	weak growth	strong growth
dnull	0.01	0.02	0.01	0.01	0.01	0.02	0.02	0.01	0.01	0.01
pfnnull	0.16	0.16	0.09	0.12	0.06	0.15	0.16	0.09	0.13	0.06
pftags	0.16	0.16	0.09	0.12	0.06	0.15	0.16	0.10	0.13	0.07
pfhd	0.16	0.16	0.09	0.12	0.06	0.16	0.17	0.10	0.13	0.07
spr12_tags	0.03	0.03	0.03	0.03	0.03	0.06	0.07	0.06	0.07	0.06
spr25_tags	0.03	0.03	0.03	0.03	0.03	0.06	0.07	0.06	0.07	0.06
spr12_hd	0.04	0.04	0.05	0.04	0.04	0.09	0.08	0.08	0.08	0.09
spr25_hd	0.04	0.04	0.05	0.04	0.04	0.09	0.08	0.08	0.08	0.09

Table 2.7: Percentage change in CE from the best, no-cost baseline strategy (pftags) and MVD (percentage change in CE per unit investment in data) for abundance estimation strategies. Some strategies have inferior magnitude of CE reduction, but superior MVD—better bang for the buck. Change in CE and MVD for growth rate estimation are not depicted because no investment in additional data improved over the best, no-cost baseline: Downing Reconstruction (dnull).

	Cost	Constant Effort		Variable Effort	
		Gross Change in CE	MVD	Gross Change in CE	MVD
		dnull	0	-	-
pfnnull	0	-	-	-	-
pftags	0	Baseline Strategy (CE = 34.5%, 20.4%)			
pfhd	1	-0.1%	-0.06%	-0.2%	-0.17%
spr12_tags	70	-59.7%	-0.85%	-45.2%	-0.65%
spr25_tags	100	-80.1%	-0.80%	-74.8%	-0.75%
spr12_hd	71	-58.6%	-0.82%	-27.8%	-0.39%
spr25_hd	101	-78.5%	-0.78%	-67.0%	-0.66%

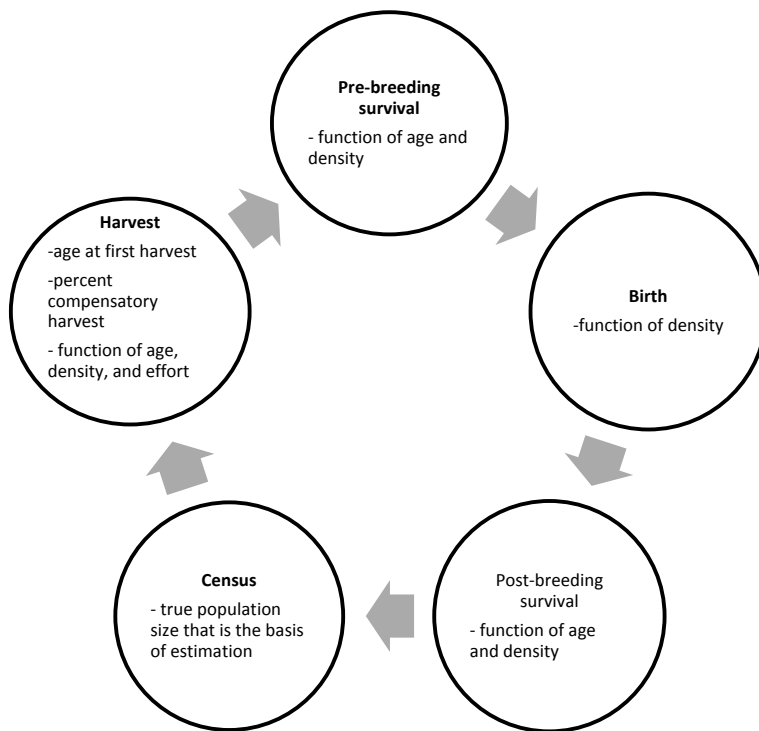


Figure 2.1: Annual cycle of events in the simulated population.

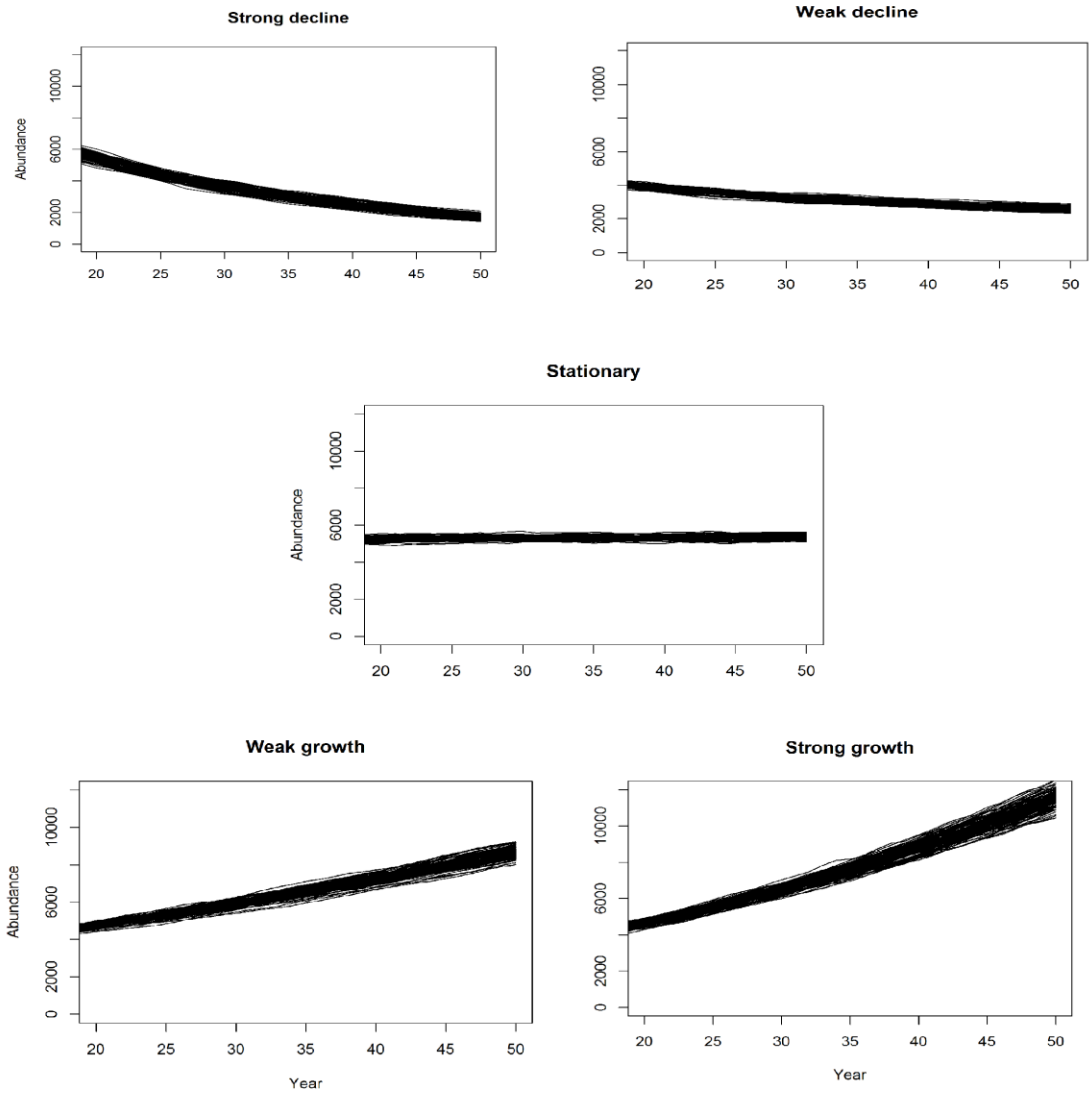


Figure 2.2: Simulated population trajectories across years 20-50.

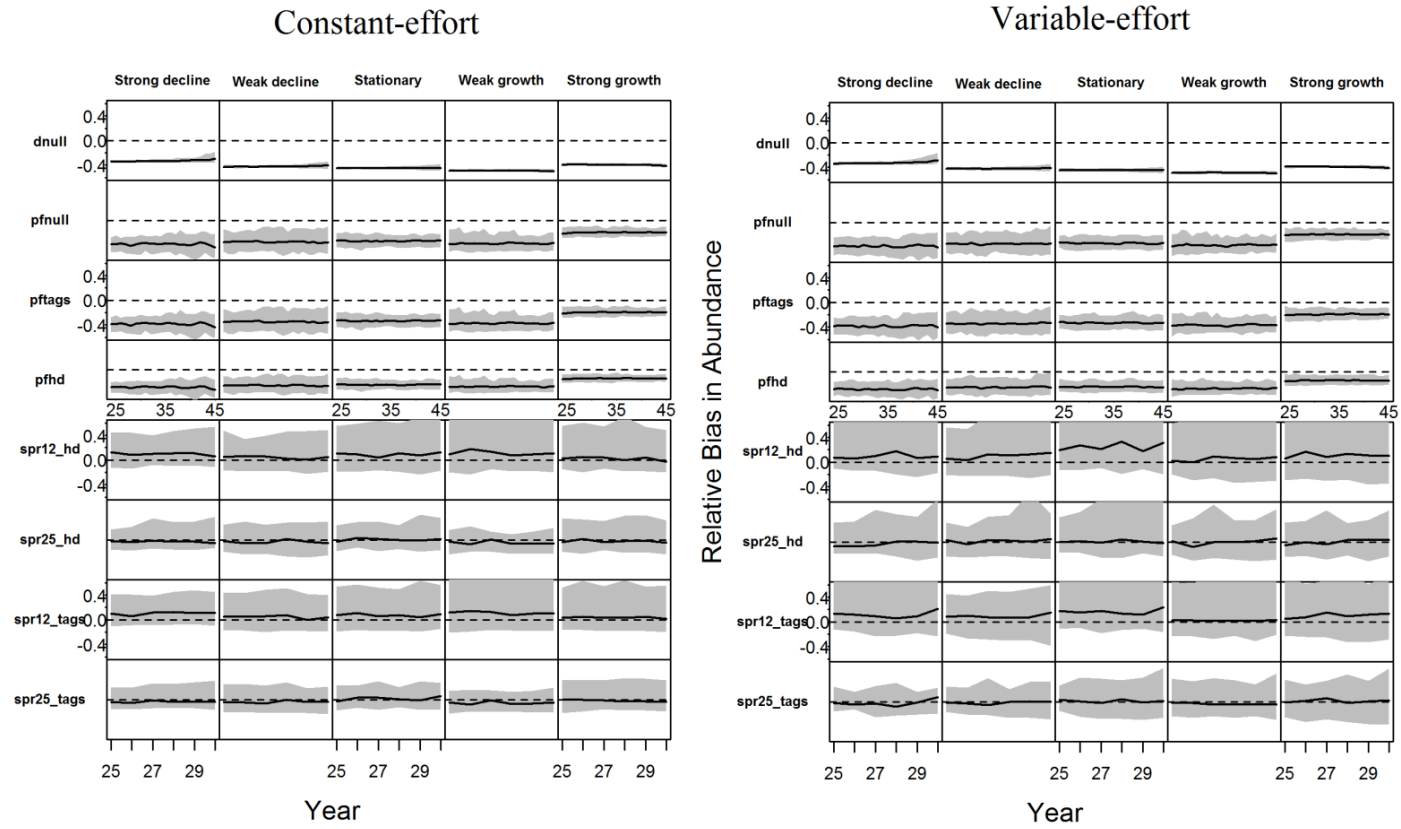


Figure 2.3: Empirical bias in abundance estimation (gray zone is 95% credible interval).

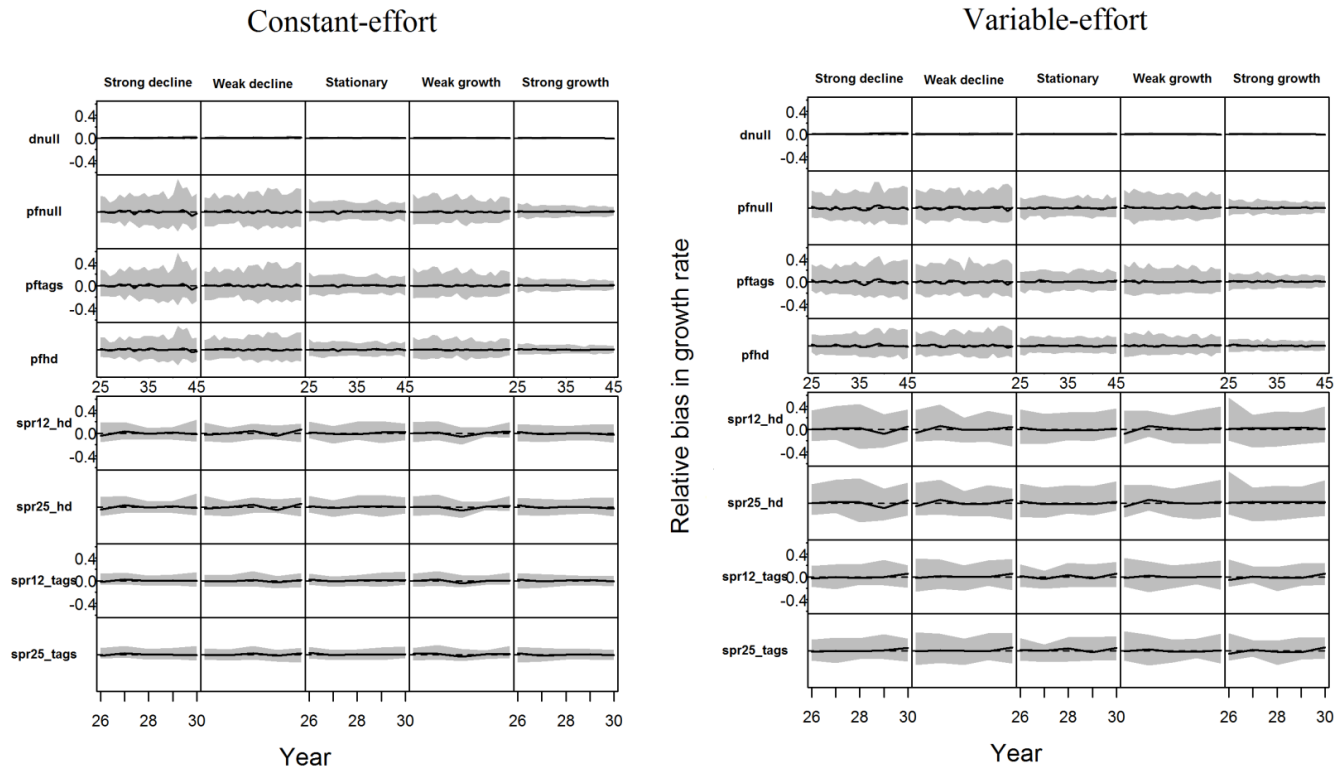


Figure 2.4: Empirical bias in growth rate estimation (gray zone is 95% credible interval).

Abundance estimation

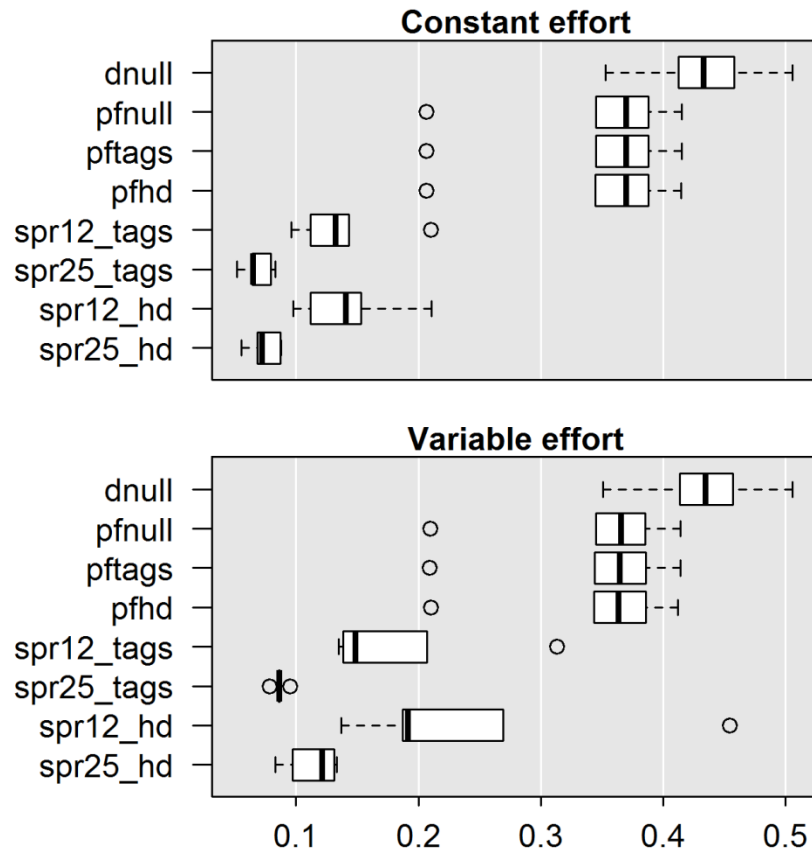


Figure 2.5: Distribution of CE values for abundance estimates.

Growth rate estimation

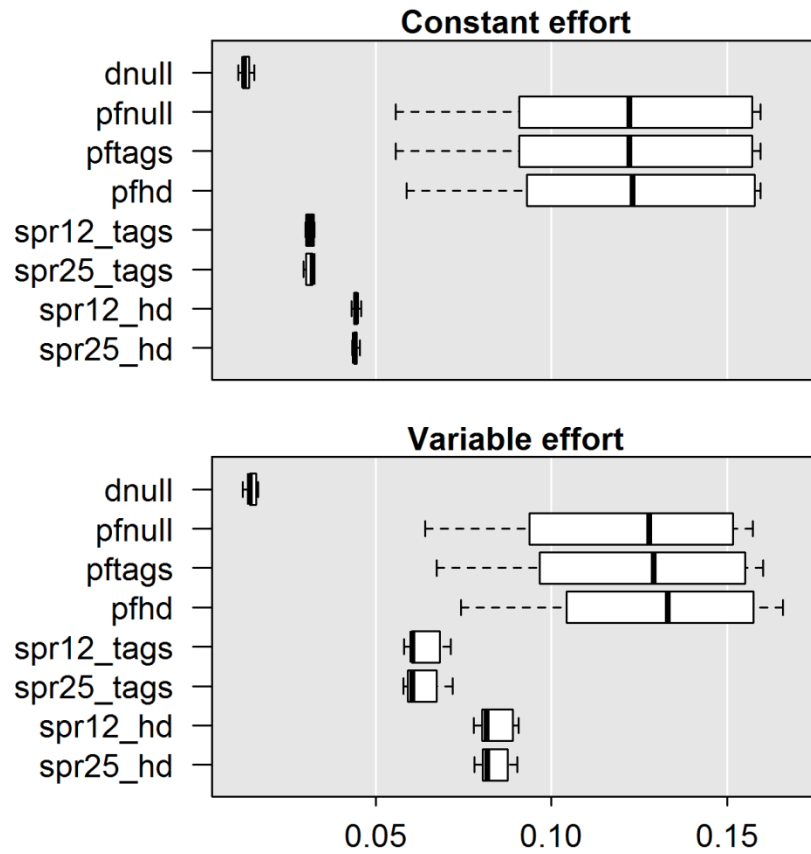


Figure 2.6: Distributions of CE values for growth rate estimates.

Chapter 3 Expected Value of Sample Information for Harvest

Management Decisions

ABSTRACT Most wildlife management decisions are made in the face of uncertainty, often induced by limited data. Population estimates are integral to many management decisions, and those estimates depend on choices of analytical methods and data to be used. Better data costs money and can improve estimates, but the realized improvements may not result in different management decisions. In this paper, we used simulated data on American black bear (*Ursus americanus*) and a hypothetical harvest management decision scenario to measure the expected value of sample information (EVSI) of a suite of different combinations of estimators and datasets (“strategies”). The strategies were built around three alternative population estimation methods: population reconstruction (Downing 1980), a change-in-sex-ratio estimator (Paloheimo and Fraser 1981), and statistical population reconstruction (Gast et al. 2013), and augmenting harvest data with hunter effort surveys and marked animal recovery data. The management decision was to raise, lower, or leave static the harvest intensity to maintain abundance within a target range. EVSI was examined across a range of uncertainty about the system state upon which decision payoffs depended. The EVSI of all estimation strategies was encouragingly large, particularly when uncertainty was greatest and a decision with no sample information had an expected value of approximately 0. Downing reconstruction had the highest EVSI at all levels of uncertainty about the true population state, followed by statistical population reconstructions. There are many reasons to invest

funds and time in collecting data, but the uncertainty clouding population management decisions can be greatly alleviated with relatively inexpensive monitoring methods.

KEY WORDS American black bear, decision analysis, EVSI, expected value of sample information, game species, harvest management, *Ursus americanus*, value of information, VOI.

State and provincial wildlife managers need to make management decisions and policy recommendations despite limited data and budgets. Because different analytical methods can result in different estimates for a given parameter, choice of analytical methods can lead to different management decisions, ultimately affecting wildlife populations. Considerable research and development has gone into creating and understanding different means of estimating wildlife populations (hereafter, "estimators"; Skalski et al. 2005). Each estimator exploits some specific kind(s) of data, and a wildlife manager chooses an estimator, but may also choose the data to use, including collecting additional data.

The fundamental data for game population analysis is "age-at-harvest data", consisting of counts by age, and typically sex, of some proportion of the harvested animals. Downing population reconstruction (Downing 1980) is an example of an estimator whose sole input is the age-at-harvest data. Other estimators, such as the Paloheimo-Fraser change-in-sex-ratio model (Paloheimo and Fraser 1981), require age-at-harvest data and can be augmented with data on hunter effort, which can be indexed by license or tag sales or estimated from more intensive hunter surveys recording tag-holder

participation rate (the proportion of hunters with tags who actively hunt) and the time spent actively hunting per participant. Additionally, mark-recapture, hunter effort, and other datasets can be used to augment age-at-harvest data in statistical population reconstructions (e.g., Skalski et al. 2007, Skalski et al. 2011). The opportunity to pair a given estimator with different datasets evokes the notion of an estimation “strategy”, an estimator combined with a particular set (or sets) of data. Wildlife managers need not only consider estimators for their existing data -- they also have the option of collecting additional data to augment that estimator or allow the use of another method. They are, in effect, choosing among estimation strategies.

Investment in intensive hunter effort or mark-recapture datasets is worthwhile if the gains from the more expensive strategy deliver benefits exceeding its cost in additional data. Often estimation strategies are evaluated in terms of statistical performance and robustness. For instance, Millsbaugh et al. (2009) used the Coefficient of Error (CE), a single metric of relative bias and precision, in their evaluation of the Sex-Age-Kill harvest-based estimator. Some researchers, such as Buderman et al. (2014), account for the financial cost of the data required by their estimation strategy. More recently, Rinehart and Donovan (Chapter 2) introduced the Marginal Value of Data, which tracks gains in statistical performance (CEs) across strategies on a per-unit-cost basis.

However, in choosing an estimation strategy, what matters most is not statistical performance, but how different strategies alter the decisions they are intended to serve. The consequences of wildlife management decisions have long-term consequences: If the harvest rate is too great, game populations can be suppressed to levels from which it may

take many years to recover (Fryxell et al. 1988, Miller 1990, Taylor et al. 2008). This is a loss of value derived from both consumptive and non-consumptive interactions with wildlife by the human constituency of management agencies. On the other hand, if the harvest rate is too little, game populations may become overabundant, contributing to disease transmission (Gortazar et al. 2006), property damage and loss (West and Parkhurst 2002, Bissonette et al. 2008), human injury (Farrell et al. 1996, Hristienko and McDonald 2007, Bissonette et al. 2008), ecological changes (Cote et al. 2004, McLaren et al. 2004, Cote 2005), and increasing the need for more intensive and expensive management tactics (Fagerstone and Clay 1997, Hristienko and McDonald 2007, DeNicola and Williams 2008, Ransom et al. 2010). Management actions based on erroneous inference of population size or trend can contribute directly to these negative outcomes. The uncertainty of our knowledge can be a major contributor to the chances that our chosen actions fail to obtain the value we seek. The value of an estimator, then, lays ultimately in the outcomes of the decisions that it supports.

Value of information (VOI) analysis is a formal means of measuring how uncertainty impacts decision outcomes, and the benefits derived from reducing that uncertainty. A typical management decision with uncertainty has several management alternatives that may be chosen, and several different system “states”. For example, a manager may have three management alternatives with respect to harvest rate: increase the harvest, decrease the harvest, or maintain the harvest (Table 3.1A). The greatest value obtained by each alternative depends on the state of the population relative to a management objective, whether the population is above the target, at the target, or below the target. The outcome, or payoff, of each alternative is state-dependent. For instance, in

Table 3.1A, if the population is above target and the harvest rate is increased (leading to population reduction), the payoff is 10 on a hypothetical value scale with higher values being more desirable than lower. Similarly, if the population is below target and the harvest rate is decreased, the payoff is also 10. However, if the population is below the target and the harvest rate is increased, the payoff is 1 because it is undesirable to increase harvest on a too-low population, driving it further below the target.

From the manager's view, the "best" alternative depends on the state of the system, but the state is uncertain at any given moment. In Table 3.1A, the manager believes that there is a 0.5 probability that the population is above target, a 0.3 probability that the population is at the target, and a 0.2 probability that the population is below target. In this case, the only information existing about the system is the probability distribution of the states. These "prior" probabilities must come from study or belief that exists prior to analyzing the decision. If the decision-maker can formulate such a probability distribution for the states, then they can calculate the expected value of each alternative as the probability-weighted sum of their payoffs, and choose the alternative with the maximum expected value. This approach is known as the expected value given prior information ("EV_{prior}"), and in Table 3.1A it is equal to 7.5.

In theory, a decision-maker who knew the true system state *before* making a decision would always choose the alternative with the greatest possible payoff. This is known as the expected value *given* perfect information (EV|PI), and in Table 3.1A it is equal to 10, the sum of the maximum payoff for each state weighted by the prior probability of each state. This number is greater than EV_{prior} and the difference between the EV|PI and the EV_{prior} is called the expected value of perfect information (EVPI; 2.5 in

Table 3.1A). EVPI measures the value that is lost to state uncertainty; a prudent decision maker would spend up to the EVPI to know the true state of the system.

A manager can never know perfectly the abundance state of a wildlife population, but through sampling and inferential statistics, they can obtain estimates of abundance and “update” their state probabilities; in doing so they can recover lost value. Akin to EVPI, the expected value of sample information (EVSI) is the difference between the expected value *given* sample information ($EV|SI$) and EV_{prior} .

$EV|SI$ can be thought of as something of a hybrid between EV_{prior} and $EV|PI$. With only prior information, the decision-maker chooses one alternative, based on its expected value under the prior probabilities. In the case of $EV|PI$, the decision-maker switches alternatives to match the situation, always choosing the “best” alternative for the state that is known with certainty. $EV|SI$ relies on making an inference based on sample information. This information is not perfect, but it may be better than nothing. Here, the decision-maker can switch alternatives (as with $EV|PI$) based on the inference about the state, but since the information is not perfect, the choice of alternatives *given the inference* is a maximum expected value decision (as with EV_{prior}). The key to the inference based on sample information is that it allows the decision-maker to update their prior probabilities.

To calculate $EV|SI$, one makes use of Bayes’ Theorem to update the prior state probabilities to a posterior probability distribution. This requires conditional probabilities, or likelihoods, of observing the sample information (i.e., sample-based

inference) under each state (Table 3.1B). These conditional probabilities of the data are found through a separate analysis of the accuracy of the inferential methods in question.

If the states are labeled A (above target), B (at target), and C (below target), with prior probabilities of $P(A)$, $P(B)$, and $P(C)$, and the sample inference is labeled “data” (i.e., the result of the estimation analysis), Bayes’ Theorem can be used to calculate the posterior probability as shown:

$$P(A|data) = \frac{P(data|A) * P(A)}{P(data|A) * P(A) + P(data|B) * P(B) + P(data|C) * P(C)}$$

Here, if $P(A)$ is the prior probability that the population is above target, then the posterior probability that the population is above target $P(A|data)$ equals the likelihood of observing the data when the population is truly above target times the prior probability the population is above target. The denominator accounts for all three states (hypotheses), where each term multiplies the likelihood of observing the data under the state multiplied by its prior probability. Bayes’ Theorem would similarly be used to calculate the posterior probabilities for $P(B)$ and $P(C)$.

Once the posterior probabilities have been calculated, then $EV|SI$ can be calculated. In our example, there are 3 possible inferences about the population: above target, at target, or below target (Table 3.1C). If the inference is “above target”, then the best alternative is the one that maximizes the expected value of the decision using the posterior probabilities that indicate the probability of that the true population is above, at, or below the target. This is the expected value of the decision *given* the inference = “above target”. The same method can be applied to the other possible inferences to get

the expected value given each possible inference. Note that the alternative that maximizes the posterior expected value is not necessarily the same from inference to inference. Now, the $EV|SI$ is the sum of these conditional expected values weighted by the probability of each inference being observed, which is the denominator of the formula for Bayes' Theorem given above. By incorporating sample information, the decision-maker may be closer to knowing the system state. EVSI, the difference between $EV|SI$ and the EV_{prior} , is a means of measuring whether that reduction in uncertainty is rewarded with increased expected value for the decision overall. In Table 3.1, $EV|SI$ is 8.8 and EVSI is 1.3.

EVSI is ideally suited to identifying the value of a given estimation strategy, not in terms of dollars or coefficients of variation (Millspaugh et al. 2009), but directly in terms of management decision payoffs. Given a choice among several estimation strategies, the best one is that which maximizes the EVSI. To quantify and interpret the decision-value of different estimation strategies to harvest management, we (1) simulated hypothetical black bear population dynamics, harvest, and data collection under five scenarios of population growth, (2) estimated abundance from the simulated data with 8 alternative estimation strategies, (3) calculated the conditional probabilities that a given strategy would correctly identify population status relative to a target abundance range (e.g., "at target" means within the range), (4) calculated the expected value of sample information for each strategy under a variety of different prior information scenarios, and (5) examined the sensitivity of our EVSI calculations to variation in key inputs. Our simulation-based approach can be applied to a wide variety of estimation methods to aid managers in evaluating potential pay-offs to investments in their monitoring systems.

METHODS

For simplicity, we will assume that our harvest management system operates with certainty. That is, the “increase harvest” alternative actually increases harvest as predicted and therefore reduces the population accordingly. We do this so that the only element of the decision that is uncertain is the state of the population at the instant of the decision.

This research was conducted by developing a population and harvest simulation model that can be parameterized to reflect a wide variety of game species and harvest regimes. Both models were functions within an R (R Core Team 2013) package called ‘AMharvest’, developed for the Vermont Fish and Wildlife Department, Vermont USA (Donovan et al. in prep). We used the function, popMod, to simulate population dynamics through time. popMod is a discrete-time population model built around an annual cycle of non-overlapping periods (Figure 3.1). The census occurred in the autumn, followed by an autumn harvest season, a post-season survival period (winter-spring), an instantaneous breeding season (spring), and pre-hunting season survival (spring/summer). The model requires inputs for several key vital rates, including harvest rate, pre-breeding survival, birth rate (offspring per breeding female per year) birth sex ratio (the proportion of offspring that are males), and post-breeding survival. For simplicity, we assumed complete reporting and no errors in sexing or aging.

For this study, we patterned the analysis after the American black bear (*Ursus americanus*) with 20 ages. Vital rates were made to fit generally the distributions documented by Beston (2011) in her meta-analysis of Black Bear demography, Bunnell and Tait (1985), and estimated harvest rates in Northern New England (F. Hammond, VT

Dept. of Fish and Wildlife, and K. Gustafson, NH Fish and Game, pers. communication).

We considered the harvest to be completely additive and cubs were excluded from the harvest by design (to match reality) and therefore from all subsequent population estimates and comparisons. Different simulation scenarios were facilitated by different parameterizations (“settings”) of age- and sex-specific vital rates (Table 3.2). Settings were chosen to produce population scenarios that were described as: stationary (finite rate of increase (λ) \approx 1.0), weak growth ($\lambda \approx$ 1.02), strong growth ($\lambda \approx$ 1.03), weak decline ($\lambda \approx$ 0.99), and strong decline ($\lambda \approx$ 0.96), which growth rates span the 95% credible interval of population growth rates identified for black bears in Eastern North America (Beston 2011). Annual harvest rates were modeled as a function of effort. We simulated annual tag sales, tag-holder participation rates, and mean days afield per active tag-holder to generate an annual count of “hunter-days” of effort that was used to generate the harvest rates for each year of simulation. Each of the 5 scenarios was simulated with variable effort and a stochastic harvest process (with both effort and the harvest process being stochastic) for a total of 10 different simulation scenarios. For each simulation, the mean tag sales, participation rates and mean days afield were constant across years at their mean values (tags = 4 (in thousands); participation rate = 0.6; days afield = 5). To generate an annual harvest rate, annual values of each quantity were drawn from normal distributions with a coefficient of variation of 10%. Then, a stochastic harvest was implemented with a binomial distribution, where the number of trials was the number of individuals available to be harvested and the harvest probability was the randomly effort variable. Each scenario was implemented in 100 iterations of 50

year simulations starting with previously determined stable age distributions (see Chapter 2 for fuller description of simulations).

Estimation strategies

We analyzed the simulated harvest data (n = 5 scenarios with 100 iterations of 50 year runs per scenario) with three types of estimation methods, each requiring different data inputs: Downing reconstruction (Downing 1980), the Paloheimo-Fraser change-in-sex-ratio estimator (Paloheimo and Fraser 1981), and statistical population reconstruction (Gove et al. 2002, Skalski et al. 2007, Skalski et al. 2011, Gast et al. 2013). SPR is not *an* estimator, but rather a type of model for estimation using multiple sources of data to jointly estimate harvest and survival parameters and different model forms are possible. We used a form in which the likelihood of the harvest and survival rates within a cohort are modeled as conditional upon the total harvest of that cohort (p.1261, Gast et al. 2013).

Each estimation method was married with various datasets into 8 different population estimation “strategies” consisting of each method matched to one or more suitable datasets (Table 3.3; see Chapter 2 for full details). The Downing method was performed using only harvest data (strategy = “dnull”, Table 3.3). The Paloheimo-Fraser method was used with 1) only harvest data and an assumed, constant level of effort applied across all years (“pfnnull”), 2) harvest data and tag sales as a proxy of effort (“pftags”), and 3) harvest data and hunter-days (“pfhd”), calculated as tag sales times mean days hunted per hunter (Table 3.3). The mean days hunted was estimated as a simple average of the responses to the simulated hunter effort survey. Residual analysis

was performed on select iterations of the Paloheimo-Fraser method. No evidence suggesting systematic lack of model fit to the data was observed.

The SPR strategies all used the same SPR model but the data differed in 2 dimensions. First, SPR strategies used either the smaller (“spr12”) or larger (“spr25”) marked animal datasets, and second, they used either tag sales as the index of effort (“tags”) or hunter-days (“hd”) as the measure of effort (Table 3.3). In the latter case, the SPR models estimated mean days hunted across all individuals in the effort survey and the product of mean days and tag sales was the estimate of hunter-days. Following the model-fitting suggestions of Skalski et al (2012), we calculated Anscombe residuals and plotted them by age and by year for select instances of our SPR estimations. The residuals gave no indication of systematic lack of fit to our data. We did not attempt to test sensitivity to annual data by dropping some years from analysis. This type of sensitivity is likely high and unavoidable in the short duration studies we simulated.

To furnish auxiliary data for SPR analysis, we simulated two tag-recovery datasets over the same 6-year period in each 50-year iteration of the simulation. One dataset had a mean capture rate of 12 animals per year and the other had a rate of 25 captures per year, representing different levels of investment and information. A Poisson random variable was drawn for the captures in each year. Captured animals were then considered tagged and the prevailing harvest and survival rates for that year and simulation setting were applied over the duration of the simulated study. We assumed the causes of mortality (harvest, non-harvest) were known with certainty and no animals were lost or censored. Males and females were equally likely to be captured. Tag

resighting occurred without error. See Chapter 2 for complete description of simulated data and estimation strategies.

For each of the five population growth scenarios, we estimated population size for each of the eight alternative strategies across the 25th to 45th years of the simulations (Chapter 2). Marked animal studies were simulated for only 6 years so SPR estimates are only available for years 25-30. Years 31-45 are therefore missing for SPR and estimates from SPR strategies is based on only 6 years of data per simulation.

Expected Value of Sample Information

To calculate the EVSI for each strategy, the prior probabilities of each state, the payoff, and the likelihood of observing the estimator result given a state are needed. We assumed that a decision maker considers three possible states of λ for the harvested species: above the target range (trueHI), at/within the target range (trueAT), and below the target range (trueLO). We assumed that the decision maker considers three possible management actions with respect to the harvest rate: increase (INCR), maintain (STAY), and decrease (DECR).

Payoffs

For the payoffs under each state and management option, we used a value scheme for the decision payoffs that consisted of an artificial variable describing the general satisfaction obtained in a given situation by the beneficiaries of the decision (Table 3.4). The scheme used a constructed scale in which the best outcome had a value of 100 and the worst outcome had a value of -200. The greater range of negative values of

undesirable outcomes relative to desirable outcomes reflects a “loss-averse” decision-maker (Kahneman and Tversky 1984), one for whom sustaining a loss (i.e., a negative payoff) is twice as bad as a gain (i.e., a positive payoff) is good. The values were assigned presuming that a population at the target level was very good, over-abundance was less good, and under-abundance was very bad. The worst values were obtained when the undesirable states, over- and under-abundance, were the result of management action, again with under-abundance being more negative than over-abundance. Arbitrary scaling is not ideal, but thoughtfully constructed, can be constructive in actual practice (e.g., Runge et al. 2011).

Prior Probabilities

We assigned the probabilities of trueHI and trueAT values ranging from 0.05 to 0.95 in increments of 0.05, and for each unique pairing with a sum less than or equal to one; we calculated $P(\text{trueLO})$ as 1 minus their sum. This resulted in 190 distinct prior distributions, each of which was used to compute the EV of a decision using only prior information (EV_{prior}) and the $EV|SI$ for each estimation strategy.

Conditional probabilities (or likelihoods)

EVSI calculations for each estimation strategy used Bayes’ Theorem to compute the posterior probability of each state, given the prior probability of each state and the likelihood, or conditional probability, of observing an estimator’s test result given each true state.

Our hypothetical management scenario represented a fall hunting season for bears in a jurisdiction with unlimited tags for state residents and a season that runs up until the

start of the fall rifle season for deer. With no tag limitations and no excess demand to hunt, means of increasing harvest are limited. The manager typically influences the harvest by modifying the end-date of the bear season to achieve greater or lesser overlap with deer season. Larger harvests occur when the bear season overlaps with deer season as the woods suddenly become full of hunters that wouldn't be out for bears otherwise. In this scenario, the bear season overlaps the first weekend of deer season and the manager can either shorten the next season to eliminate that overlap and reduce the harvest, lengthen the season into the first week of the deer season to increase the harvest, or make no changes to keep the harvest at the same level. These alternatives are referred to as "DECR" for decrease the harvest, "INCR" for increase, and "STAY" for maintain the current harvest level.

We framed the population monitoring task as a classification "test" with the possible inferences ("results") of the population as above, at, or below a defined target range. We assumed that in year t , the existing abundance is optimal relative to some hypothetical ecological and social standards such as ample hunting and viewing opportunities, minimal nuisance events, etc. Therefore, the abundance estimate for year t is the target abundance. We then project ourselves 4 years into the future (year = $t + 4$) and estimate the annualized growth rate since year t . We considered that the population warranted management if the annualized growth rate estimated 4 years later ($T + 4$) was greater than 1.019 or less than .981, approximating a 10% change in the population over 5 years. Estimated growth rates within the defined target zone (test result = "testAT") indicated that the population was at the target level and the optimal management action should be to maintain the status quo harvest intensity. If the estimated growth rate was

above the target zone (“testHI”), the management decision would be to intensify harvest through some defined measures such as extended seasons, expanded tag offerings, etc. An annualized growth rate below the zone (“testLO”) would indicate the need for restricting the harvest intensity to ameliorate the population decline. Thus, “testAT”, “testHI”, and “testLo” represent the inference obtained via an estimator strategy.

The simulation study produced abundance estimates for years 25-45 of each iteration from all estimation strategies except SPR. We had 6 years of SPR estimates for each iteration due to the limitations of the data those strategies employ. For a given estimation strategy, we selected 5 4-year periods at random from each iteration of the simulation, and computed the annualized growth rate based on the estimated abundances. We also computed the growth rate based on the true (simulated) abundances for the same periods. The estimated growth rates were classified as “testHI”, “testAT”, or “testLO”, depending on if the growth rate was above, within, or below the target range of 0.981 to 1.019. Similarly, we classified the true growth rate as “trueHI”, “trueAT”, “trueLO”, by the same criteria, so that for a sample from each iteration, we knew both the test result and the true state. Compiling these across the all iterations of all settings in the simulation study, we computed the conditional probabilities of each test result given each true state as a proportion of random samples. For example, using the Downing reconstruction strategy (“dnull”), 82% of the “trueHI” samples were both “testHI” and “trueHI”, so $P(\text{testHI} \mid \text{trueHI})_{\text{dnull}} = 0.82$. This process was followed for all estimation strategies, in turn.

We used the payoffs and conditional probabilities of the test results to calculate the EV|SI across a range of different prior distributions for the states (see Appendix A).

Subtracting each EV_{prior} from the corresponding $EV|SI$, we found the EVSI for each strategy across all sets of prior probabilities. For comparison, we computed the maximum and median values of EVSI for each strategy across all prior distributions.

Sensitivity Analysis

We formulated six different payoff matrices to examine the sensitivity of EVSI to the variation among payoffs in the matrix (Table 3.9). Matrices varied by absolute range of values across all outcomes and range of difference between outcomes. Most matrices ranged from 0 to 100. Had we set the lowest payoff to, say, 50, this would serve to rescale the matrix, but the important aspect of the matrix to examine is the effect of the relative distribution of scores within a given range. We performed the EVSI calculations using each payoff matrix in turn and compared ranges and distributions of resulting EVSI values among matrices. The sensitivity analysis of conditional probabilities was implicit in our analysis as the estimation methods we examined displayed a range of distributions of conditional probabilities of correct diagnosis of population states. Therefore, we examined the impact of different conditional probability distributions through examining patterns in EVSI among the estimation strategies.

RESULTS

The growth rates for the five base population simulations were approximately 0.96 (strong decline), 0.99 (weak decline), 1.0 (stationary), 1.02 (weak increase), and 1.03 (strong increase; Table 3.3). Effort for all years of variable-effort simulations ranged between 2.27 and 5.8 thousand tags (mean = 4, sd = 0.4) and between 5 and 24 thousand hunter-days (mean = 12, sd = 2). The correlation between tags and hunter-days was 0.58.

Nominal harvest rates (calculated at the intercept, without covariates) varied between 0.05 and 0.08 for females and 0.08 and 0.13 for males. Positive age effects result in pre-breeding survival between 0.90 and 1.0 for adults, and post-breeding survival rates between 0.80 and 0.85 for males and 0.85 and 0.88 for females. Annual birth rates ranged between 1.03 and 1.22 cubs per breeding-age female per year.

Conditional probabilities

The conditional probabilities of the estimation strategies (Table 3.5) were generally better for the trueHI and trueLO states than for trueAT. Probabilities of correct state identification varied from 0.6 (pfhd) to 0.82 (dnull) when population was truly above the target (“trueHI”), from 0.32 (pftags) to 0.89 (dnull) when the population was at the target (“trueAT”), and from 0.61 (pftags) to 0.92 (dnull) when the population was below the target (“trueLO”). All strategies performed better when the true state was above or below the target. The Paloheimo-Fraser strategies, in particular, had essentially uniform probabilities for results when the population was at the target. The abundance estimates from the Paloheimo-Fraser strategies were the most variable of all strategies (Chapter 2) and on a scale that apparently exceeded the target zone, making them unreliable at this level of growth rate monitoring. The SPR strategies were better than Paloheimo-Fraser in this regard, but not as good as Downing reconstruction. The probabilities of correct state identification given that the population was at the target zone varied from 0.32 (pf_tags) to 0.89 (dnull) across the SPR strategies, with the tag-only strategies performing generally better than the hunter-days strategies.

The Paloheimo-Fraser strategies were sufficiently similar to each other, as were the SPR strategies, that the remainder of this chapter focuses on only the *dnull*, *pftags*, and *spr25_tags* strategies, with the latter two representing all strategies using the same estimators.

Expected value of sample information

Recall that $EV|SI$ is the expected value a decision-maker could achieve using inferences based on the sample information and these values will tend to fall between EV_{prior} and $EV|PI$ and are directly comparable to those two quantities. $EVSI$, on the other hand, might take high or low values and is not comparable to EV_{prior} or $EV|SI$. Rather, $EVSI$ is comparable to $EVPI$. $EVSI$ will be low where EV_{prior} is relatively close to $EV|SI$ and $EVSI$ will tend to be great where EV_{prior} and $EV|SI$ diverge, generally because the former gets very small. A small value of $EV|SI$ means that the outcome of the decision will be slight, whereas a small value of $EVSI$ means that little additional benefit is obtained from the sample inference, but it tells us nothing directly about the expected outcome of the decision, with or without sample information. Hence, we discuss both the $EV|SI$ and the $EVSI$ in the following sections.

Across the examined range of possible prior distributions, EV_{prior} ranged from 0 to 82.5 with values being least when uncertainty about state is greatest (Figure 3.2). The situations with very low EV are most likely driven by only one alternative for a given state having a positive payoff. When the prior probabilities of the 3 states are uniform ($P(\text{trueHI}) = P(\text{trueAT}) = P(\text{trueLO}) = 0.333$), the expected value of an alternative is a simple average across the payoffs for the states. On the other hand, an outcome of 0 can

be interpreted as “neutral”, given that our loss-averse payoff scheme ranges from +100 to -200. Given the down-side risk of negative payoffs, obtaining neutral outcomes in uncertain situations could be counted as a victory of sorts.

The $EV|PI$ is 100 for all prior distributions as the best payoff per state is +100 in all cases, rendering the prior distribution immaterial. If the states had different maximum payoffs, then $EV|PI$ would be more sensitive to the prior distribution. With $EV|PI$ fixed at 100, $EVPI$ varied inversely to EV_{prior} , being high when EV_{prior} was low and vice versa. EV_{prior} is lowest and $EVPI$ is highest when prior uncertainty is greatest, as indicated by uniform prior probabilities $P(\text{trueAT}) = P(\text{trueHI}) = P(\text{trueLO}) = 0.333$. $EVPI$ reaches a low of 8.5 when $P(\text{trueAT})$ was 0.95, $P(\text{trueHI})$ was 0.05, and $P(\text{trueLO})$ was 0. In other words, the value of perfect knowledge is proportional to uncertainty, or conversely, EV_{prior} is inversely proportional to uncertainty. EV_{prior} was highest as one of the state probabilities approached 1, which led to low values of $EVPI$. When prior uncertainty was greatest (prior state probabilities \sim equal), EV_{prior} hovered near zero, leading to the greatest values of $EVPI$.

With sample information obtained from an estimation strategy, the priors are updated via Bayes' Theorem, and $EV|SI$ and $EVSI$ can be computed. Each of the three estimation strategies had high $EVSI$ under some combinations of priors, but they differed in the overall magnitude.

$EV|SI$ with Downing reconstruction ranged from 75 to 92 with a median of 82 (Table 3.6). When uncertainty was low (e.g. $P(\text{trueAT}) = 0.95$), the $EV|SI$ of Downing was approximately equal to EV_{prior} , confirming that inference based on sample

information is of little value in such situations. On the other hand, when uncertainty was high, the $EV|SI$ of Downing reconstruction was much greater than EV_{prior} . When $P(\text{trueAT}) = P(\text{trueHI}) = 0.3$, $EV|SI$ was 80 and EV_{prior} was 0.4, yielding EVSI of more than 79 (Figure 3.2). As noted above, the $EV|PI$ was 100 for all cases, so this estimation strategy was excellent for monitoring the population relative to the target.

Paloheimo-Fraser had maximum $EV|SI$ around 92, a minimum of 8, and median $EV|SI$ of 37. In situations of high prior uncertainty, the $EV|SI$ with Paloheimo-Fraser was between 8 and 20 (Table 3.7), not a great deal more than the very low EV_{prior} in such situations. SPR had $EV|SI$ values that ranged between 37 and 93 with a median of 50 (Table 3.8).

The highest EV_{prior} and $EV|SI$ (all strategies) values were in the cases of low uncertainty, as in the corners of the images in Figure 3.2. Therefore, the highest $EV|SI$ values did not contribute to high EVSI. Rather, the highest EVSI values come from the *lower* values of $EV|SI$ for a given estimation strategy. Because all methods tend to be lowest when uncertainty is high, the question then becomes, how low does each strategy go?

As indicated by EVSI, Downing reconstruction was twice as good as SPR and 4-8 times better than Paloheimo-Fraser at reducing state uncertainty when prior information was weakest. For any given prior state distribution, EVSI was greatest for Downing, less for SPR, and least for Paloheimo-Fraser. This pattern is also evident in the median EVSI values for each estimator across all prior distributions (Figure 3.3). The EVSI for Downing reconstruction was surprisingly great, approaching $EV|PI$.

EVSI sensitivity

The payoff matrices (Table 3.9) examined did not change the relative efficacy of the estimation strategies, but different matrices did result in different distributions of EVSI values. The different payoff matrices can be compared directly when their values are normalized to a 0 – 1 scale (Figure 3.4, Figure 3.5). For a given estimation strategy, the distribution of EVSI values across different priors changes and the greater the range of values in the payoff matrix, the greater the range of EVSI (Figure 3.4). In Figure 3.5, the top row shows the EVSI for *dnull*, *pftags*, and *spr25_tags* under the risk averse payoff, with *dnull* offering the highest and *pftags* the lowest values, generally. The same is true for these models under the *slight3* payoffs (Figure 3.5, bottom row) although, again, the absolute range of values is lesser under this payoff scheme.

The range of difference in the payoff values influences the range of EVSI by altering the scale of the EV_{prior} and $EV|SI$. Because the payoffs scale EV_{prior} and $EV|SI$ similarly, the relative magnitude of EVSI between estimation strategies (which is “better”) is unaffected. As reported above, the “risk averse” matrix resulted in median $EV|SI$ for *dnull* and *pftags* of 85 and 35, respectively. Using the “*slight3*” matrix with payoffs of 0, 75, or 100, the median $EV|SI$ for *dnull* and *pftags* were 97 and 88. The differences between the strategies are less in the latter case because the penalties for “wrong” action are less, but the same strategy delivers the higher expected value in both cases. This pattern holds with the other matrices as well: range of $EV|SI$ values is roughly proportional to the relative distribution of payoffs within the matrix (Figure 3.4). *Slight3* has relatively high payoffs for most sub-optimal decisions while the risk averse matrix penalizes “wrong” decisions, so in the former case, the manager would obtain a relatively

high value from 2 of the 3 alternatives for each state. In the latter, risk averse case, low values are more common than high ones, which appear to expand the overall range of EV|SI scores. The “positive” payoff matrix only rewards one alternative for each state (100) compared to payoffs of 0 for all other alternatives. Nevertheless, this does not span the same range as the risk averse matrix and so the overall range of EV|SI is lesser than risk averse and greater than slight3.

The conditional probabilities of accurately diagnosing the true population state from among three options could vary, for any hypothetical estimation strategy, from complete certainty (e.g., 1, 0, 0) to complete uncertainty (e.g., 0.33, 0.33, 0.33). The conditional probabilities of the dnull model typically strongly favored one state (e.g. 0.82, 0.18, 0.00). Those of pftags were often close to uniform (e.g., 0.34, 0.32, 0.34), and those of spr25_tags were intermediate (e.g., 0.18, 0.55, 0.27).

The conditional probabilities influence the magnitude of the EVSI for a given strategy. Ultimately, this is what differentiates the ranges of EVSI for different strategies (Figure 3.5). Less certainty in the conditional probabilities means that less information is added to the prior, hence the generally low values of EVSI for pftags. Downing reconstruction (dnull) had the greatest EVSI values because it delivered the greatest certainty of proper state identification.

DISCUSSION

Population estimators are typically evaluated on the basis of their statistical performance, either under ideal conditions, or under violations of assumptions. Value of information analysis parallels the results from the statistical and cost-performance

analyses, but renders the issue directly in terms of the decision to be made. In those terms, all of the strategies effectively reduced uncertainty, thereby increasing the expected return on the decision. The best performer, Downing reconstruction (dnull), is also the least expensive in practice. SPR methods, which also performed well, are the most costly as they require auxiliary data to shed a different light on harvest and survival processes. In this study, such expense appears unjustified purely from the standpoint of harvest management decision-making.

Expected value of sample information is an incisive analysis for characterizing the benefit to be gained from data collection and analysis when there is a decision problem to evaluate. In this case, we used a hypothetical management scenario that was based on identifying the growth rate in a population across a small time frame. This scenario will clearly favor estimation strategies that excel in identifying growth rates at the expense of those that are better at estimating abundance. However, growth rates are based on abundance estimates. Repeating this analysis with a management scenario that focuses on abundance will deliver the same results as long as the decision is based on a comparison of abundance estimates at two points in time (unpublished analysis). The growth rate as used here is simply a scaling of change in abundance relative to the initial abundance.

The management scenario that is not addressed by this analysis is that of managing for a specific abundance that is identified “outside” the estimation strategies in question. That is, the operative element of our hypothetical scenario is not a choice between growth rate or abundance, but rather the idea that the management target can be identified by some means (e.g., assessments of constituent satisfaction,

ecological/population health, nuisance/danger, etc) and then an estimated abundance can be assigned to that moment in time as a benchmark against which to judge the need for management (i.e., internally-consistent). As long as that is possible, then the management decisions will be inherently based on changes from baseline. If, on the other hand, a numerical abundance target were defined by some other means, then ability to estimate abundance with great fidelity takes on a different character as do the requirements of the estimation strategies. In that case, the more expensive estimation strategies would be more valuable to the manager and this should be reflected in an EVSI analysis of such a decision problem.

Had the best EVSI resulted from one of the estimation strategies that carried substantial cost of acquiring data, the wildlife manager would need to compare the gain in EV of the decision to the financial cost of that method. In such a case, the construction of the payoff matrix takes on particular importance. If a payoff matrix can be constructed with payoffs in dollars, then a given estimation strategy is beneficial if its cost is less than the EVSI. With an arbitrary payoff matrix, such evaluation is not as obvious. A manager would have to use other means to determine how many dollars might be spent to achieve a +80 “satisfaction” based on EVSI. Although this is not a trivial challenge, neither is it completely unprecedented. In practice, harvest management often includes nuanced evaluations of both quantitative and qualitative data and subjective assessments where data are lacking. Managers must balance the desires of a constituency whose preferences are largely hidden and formulating a quantitative yard-stick of success is challenging. Some citizens desire higher harvest rates or better chances at success. Others prefer lowered harvest and other modes of appreciating wildlife. These and other challenges

lead to management that is a mix of information and analysis that often defies purely quantitative, let alone fiscal, evaluation. Of course, there are means of elucidating even “satisfaction” with rigor and even coarse payoff matrices can be helpful.

The value of a population estimation and monitoring strategy is clearest when the truth is most obscure: this is exactly when knowing something more can make the biggest difference in expected outcomes. All of the examined strategies had positive EVSI, but of different magnitudes. When prior state uncertainty was greatest, the EVSI of Downing reconstruction attained nearly 80% of the EVPI, and at no additional expense (e.g. data collection). The other methods, using varying degrees of additional data, performed, at best, only half as well.

We used an internally-consistent population-monitoring scheme in which the target and the subsequent monitoring were both defined by a given strategy. Employing our hypothetical decision scenario would require waiting for several years after management actions are made to re-evaluate the population state. Most estimation methods are sensitive to non-stable harvest rates so using them over a period with known changes in harvest rate is not advised. Simple estimation strategies can perform quite well as long as the underlying population and harvest processes are not changing. The Downing reconstruction is known to be strongly negatively biased (Davis et al. 2007, Chapter 2), yet consistently so, making it excellent for tracking population trends. This would not be the case when the harvest system is unstable, as when harvest rates have abrupt changes or temporal trends. Downing and Paloheimo-Fraser assume constant harvest and survival rates across the period represented by the data. In that case, a

strategy such as SPR may come to the fore. SPR is the best of all examined strategies at estimating abundance (Chapter 2), but it is also costly.

Fieberg, et al (2010) found SPR-type models superior to Downing in tracking trends. Their study found similar degrees of error for Downing as we did (e.g. MSE = 0.009; Chapter 2) while their integrated models performed much better (e.g. MSE = 0.00005). Based on the value of information analysis presented here, there may be little room to improve on the Downing reconstruction when it comes to maximizing expected value of management decisions. The real strength of SPR is likely to emerge when underlying conditions make the assumptions of simpler methods untenable or when suitable data already exist or are being collected to support other research objectives as well. Our emphasis here was to examine scope for reducing decision uncertainty under small-budget and small-sample conditions, and we did not provide a comprehensive look at the potential benefits of all estimation strategies. Given our focus on small-sample scenarios, we found the Downing method to be superior to the other strategies.

The Downing Reconstruction is not a panacea, however. Managing from only the information it conveys could lead to mismanagement. If a game population is in decline, and the individual vulnerability to harvest is increasing, the resulting harvest could be relatively stationary over many years. This stability in the harvest would mask the actual over-harvest that was occurring. In such a case, additional information is necessary to contextualize the reconstruction information. The ability to accurately and precisely estimate abundance is valuable here, as is the ability to collect a wide range of other information that game managers rely on to formulate as complete a picture as possible of the population of concern. Clearly there a wide range of information is needed when

managing a game population, but our analysis suggest that a substantial portion of the year-over-year monitoring for harvest management may be relatively simple. More intensive and expensive methods might have a role intermittently do identify the general range of current abundance (too high, too low).

Our analysis also showed that the results were robust to how the payoff values are encoded. We duplicated these analyses using alternate sets of values and compared the effect of different conditional probability distributions. In general, the less difference in payoff value between alternatives, the less difference there is between estimation strategies. If all or most alternatives are relatively high in value, the EV|SI scores will be relatively high. EV_{prior} follows this same scaling such that the resulting EVSI values get smaller and smaller as the difference among alternative decreases. The conditional probabilities shift the relationship between EVSI and the prior probabilities.

As a means of comparing estimation strategies, EV|SI and EVSI are robust to different constellations of payoffs and conditional probabilities. For a single estimation strategy and the question of whether the gain in decision value is worth additional investment in data, the details will matter. In particular, the lowest values of EVSI will occur at different prior probabilities as the conditional probabilities change. Uncertainty of conditional probabilities can be addressed through Monte Carlo simulations of the EVSI over a range of possible values. This would allow generation of confidence distributions around the EVSI values of a given estimation strategy. Payoff uncertainties could be handled similarly.

MANAGEMENT IMPLICATIONS

When management of game populations is based on tracking trends, simple methods with inexpensive data are more than adequate. Provided their use is justifiable, they provide the biggest bang for the buck in terms of reducing the uncertainty that erodes the expected long-term payoffs of management decisions.

All strategies examined in this study were effective at tracking growth rates, leading to positive EVSI values. The Downing offered the greatest EVSI values for the least cost and complexity. The volatility of the Paloheimo-Fraser method suggests caution in its use. The Paloheimo-Fraser strategies basically indicated that the population was above or below the target zone for most years, even when the true population was on target. These strategies had limited ability to shed light on the true state when prior uncertainty was high. Use of these strategies would depend on other measures to guard against false classifications. In actual practice, longer time-series, additional streams of information, and expert judgment will be available, and in this case, required. Finally, SPR can be an excellent tool for more incisive population analysis than is possible with non-statistical reconstructions, but does not confer the same EVSI as other, much cheaper methods.

The value of information analysis presented here underscores the differences between estimating abundance and monitoring populations over time. Estimating abundance with precision and accuracy is costly, while even the least costly means of monitoring trends can radically reduce the uncertainty faced by wildlife management decision-makers. When the upper limits of the wildlife population are defined primarily by human/social drivers, rather than ecological, the task of providing precise and accurate

estimates of abundance may, in fact, be meaningless to management decision-making. The uncertainty that erodes value in management decisions is not whether there are 5000 or 6000 animals. Rather it is where the population stands relative to some previously-defined target. It is possible to effectively manage a population without knowing precisely how large it is, as long as targets can be defined and monitored over time.

Given the established performance of low-cost estimation methods, the vital task becomes identifying adherence to or departure from model assumptions. In the long run, a mixed strategy is likely the best: periodic investment in intensive data to test assumptions (which might be useful for 'benchmark' abundance estimates), within a regular program of low-cost annual trend-tracking that we have shown can greatly reduce the value lost due to uncertainty. Managers would also do well to grapple with how their decisions might change if uncertainty is reduced because some sources of uncertainty may not be obstacles to better decisions.

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FIGURE LEGEND

Figure 3.1: Annual cycle of events in the population as simulated using popMod.

Figure 3.2: Expected values under a range of prior distributions. Lighter colors indicate higher values: a) expected value with only prior information (EV_{prior}), b) EVSI using Downing reconstruction, c) EVSI using Paloheimo-Fraser, and d) EVSI using SPR. Note that the EVSI values for each estimation strategy are the values of $EV|SI$ minus the EV_{prior} (chart a). EV_{prior} and $EV|SI$ values are also shown in Tables 3.6-3.8.

Figure 3.3: Maximum and median EVSI for three representative strategies. Statistics calculated across 190 different prior state distributions.

Table 3.1: Example quantities and calculations used in expected value of sample information analysis. A) Expected value with only prior information (EV_{prior}) and EVPI. B) Conditional likelihoods representing accuracy of inference based on the sample information. C) The individual expected value calculations under each possible inference. D) EV|SI resulting from probability-weighted sum of the inference-specific expected values and EVSI, the value gained by using the sample information.

		Alternatives: change harvest intensity			
		Prior Probability	Increase	Maintain	Decrease
A)	State				
	Above Target	0.5	10	7	5
	At Target	0.3	7	10	7
	Below Target	0.2	1	5	10
	EV(alternative)		7.3	7.5	6.6
	EV_{prior}		7.5		
	EV PI		10		
	EVPI		2.5		

		Likelihood of inference		
		Above Target	At Target	Below Target
B)	State			
	Above Target	0.7	0.2	0.1
	At Target	0.15	0.7	0.15
	Below Target	0.1	0.2	0.7

		Alternative harvest regimes			
		Posterior Probability	Increase	Maintain	Decrease
Inference = Above Target					
C)	State				
	Above Target	0.84	10	7	5
	At Target	0.11	7	10	7
	Below Target	0.05	1	5	10
	EV(alternative inference)		9.2	7.2	5.5
	EV(Infer Above Target)		9.2		

		Alternative harvest regimes			
		Posterior Probability	Increase	Maintain	Decrease
Inference = At Target					
C)	State				
	Above Target	0.29	10	7	5
	At Target	0.60	7	10	7
	Below Target	0.11	1	5	10
	EV(alternative inference)		7.2	8.6	6.8
	EV(Infer At Target)		8.6		

		Alternative harvest regimes			
		Posterior Probability	Increase	Maintain	Decrease
Inference = Below Target					
C)	State				
	Above Target	0.21	10	7	5
	At Target	0.19	7	10	7
	Below Target	0.60	1	5	10
	EV(alternative inference)		4.1	6.4	8.4
	EV(Infer Below Target)		8.4		

D)	EV SI	8.8
	EVSI	1.3

Table 3.2: Parameter values used for simulating vital and harvest rates. Sample rates, calculated at the intercept, are displayed. Birth sex ratio was modeled as 1:1 for all simulation scenarios.

Simulation sub-model		Simulation scenarios				
		strong decline	weak decline	stationary	weak increase	strong increase
Female Harvest rate (logistic)	value at intercept:	0.08	0.06	0.05	0.05	0.05
	intercept	-2.4	-2.7	-2.9	-3	-3
	age	0.02	0.02	0.02	0.02	0.02
	age squared	-0.002	-0.002	-0.002	-0.002	-0.002
	density		0.01		0.01	0.01
	effort	0.035	0.035	0.035	0.035	0.035
Male Harvest rate (logistic)	value at intercept:	0.13	0.10	0.10	0.08	0.12
	intercept	-1.9	-2.2	-2.2	-2.5	-2
	age	0.02	0.02	0.02	0.02	0.02
	age squared	-0.002	-0.002	-0.002	-0.002	-0.002
	density		0.01		0.01	0.01
	effort	0.035	0.035	0.035	0.035	0.035
Female Post-breeding survival (logistic)	value at intercept:	0.85	0.88	0.88	0.88	0.88
	intercept	1.7	2	2	2	2
	age	0.2	0.2	0.2	0.2	0.2
	age squared	-0.005	-0.006	-0.005	-0.006	-0.006
	density		-0.005	-0.05	-0.005	-0.005
	effort	0.80	0.85	0.85	0.85	0.85
Male Post-breeding survival (logistic)	value at intercept:	0.80	0.85	0.85	0.85	0.85
	intercept	1.4	1.7	1.7	1.7	1.7
	age	0.2	0.2	0.2	0.2	0.2
	age squared	-0.005	-0.006	-0.005	-0.006	-0.006
	density		-0.005	-0.05	-0.005	-0.005
	effort	1.03	1.16	1.22	1.22	1.08
Birth rate (cubs/female/year) (Poisson)	value at intercept:	1.03	1.16	1.22	1.22	1.08
	intercept	0.03	0.15	0.2	0.2	0.08
	density		-0.008	-0.008		
	density squared	-0.001	-0.005	-0.005		-0.001

Table 3.3: The 8 alternative estimation strategies. As one moves downward through the table, the strategies include increasing sophistication of estimator and intensity of data. The ‘pfnll’ strategy assumes constant annual effort, ‘pftags’ uses tag sales as the index of effort, and ‘pfhd’ uses hunter-days, calculated as the product of tag sales and the mean days hunted as reported on hunter surveys. The statistical population reconstructions differ in 2 dimensions. First, they use either the smaller or larger marked animal datasets, and second, they use either tag sales as the index of effort, or mean days hunted were estimated jointly with other parameters and used with tag sales to calculate hunter-days as the index of effort.

Name	Estimator	Harvest data	Tag Sales	Hunter Effort	Marked Animal Data	
					Small (12)	Large (25)
dnull	Downing Reconstruction	x				
pfnll	Paloheimo-Fraser	x				
pftags	Paloheimo-Fraser	x	x			
pfhd	Paloheimo-Fraser	x	x	x		
spr12_tags	Statistical Population Reconstruction	x	x		x	
spr25_tags	Statistical Population Reconstruction	x	x			x
spr12_hd	Statistical Population Reconstruction	x	x	x	x	
spr25_hd	Statistical Population Reconstruction	x	x	x		x

Table 3.4: Payoff values associated with each combination of state and alternative. This scheme is “loss-averse”. Mismanagement (e.g. increasing harvest on a population that is already below the target) is twice as bad as proper management (decreasing harvest when the population is too low) is good. The best decision outcomes are valued at 100 while the worst outcome (increasing harvest intensity on a population is actually below the management threshold) has a value of -200.

States	Alternatives		
	INCR	STAY	DECR
trueHI	100	-50	-100
trueAT	-100	100	-50
trueLO	-200	-100	100

Table 3.5: Conditional probabilities of eight different estimation strategies, given the true states: $P(\text{Result}|\text{State})$. For each strategy, the values for a given state add to 1. For Downing reconstruction (dnull), the $P(\text{testHI}|\text{trueHI}) = 0.82$, meaning that 82% of the time that the true population is above the management target, this estimator correctly identified the true state.

Result	State	dnull	pfnnull	pftags	pfhd	spr12_hd	spr25_hd	spr75_hd	spr12_tags	spr25_tags	spr75_tags
testHI	trueHI	0.82	0.62	0.62	0.6	0.62	0.65	0.63	0.69	0.69	0.69
testAT	trueHI	0.18	0.31	0.3	0.3	0.31	0.28	0.29	0.27	0.26	0.27
testLO	trueHI	0	0.08	0.08	0.1	0.07	0.07	0.07	0.04	0.05	0.05
testHI	trueAT	0.03	0.34	0.34	0.34	0.26	0.27	0.25	0.18	0.18	0.18
testAT	trueAT	0.89	0.32	0.32	0.32	0.39	0.41	0.41	0.55	0.56	0.55
testLO	trueAT	0.07	0.34	0.34	0.35	0.35	0.32	0.33	0.26	0.26	0.27
testHI	trueLO	0	0.16	0.16	0.17	0.05	0.06	0.06	0.02	0.02	0.02
testAT	trueLO	0.08	0.21	0.22	0.2	0.27	0.25	0.26	0.21	0.22	0.22
testLO	trueLO	0.92	0.63	0.61	0.63	0.68	0.69	0.68	0.77	0.76	0.77

Table 3.6: Expected value *given* sample information (EV|SI) for Downing reconstruction (dnull) across a range of prior distributions. Columns differ by the probability that the population is truly at the target, P(trueAT). Rows differ as the probability that true stat is above the target, P(trueHI). The remaining probability, P(trueLO), is defined as 1 minus the sum of P(trueAT) and P(trueHI). Note that with this strategy, EV|SI remains great when the prior state probabilities tend to equality (i.e., maximal uncertainty).

P(trueHI)	P(trueAT)																		
	0.05	0.10	0.15	0.20	0.25	0.30	0.35	0.40	0.45	0.50	0.55	0.60	0.65	0.70	0.75	0.80	0.85	0.90	0.95
0.05	90.7	83.3	83.2	83.1	83.1	83.0	82.9	82.8	82.8	82.7	82.6	82.5	82.5	82.4	82.3	82.2	82.2	82.4	92.0
0.10	88.9	82.8	82.7	82.6	82.5	82.5	82.4	82.3	82.2	82.2	82.1	82.0	81.9	81.9	81.8	81.7	81.6	91.0	
0.15	87.0	82.2	82.1	82.1	82.0	81.9	81.8	81.7	81.7	81.6	81.5	81.5	81.4	81.3	81.2	81.1	90.0		
0.20	85.3	81.6	81.6	81.5	81.4	81.3	81.3	81.2	81.1	81.0	81.0	80.9	80.8	80.7	80.7	80.7	89.0		
0.25	83.4	81.1	81.0	81.0	80.9	80.8	80.7	80.6	80.6	80.5	80.4	80.4	80.3	80.2	80.2	88.0			
0.30	81.6	80.6	80.5	80.4	80.3	80.3	80.2	80.1	80.0	79.9	79.9	79.8	79.7	79.7	87.0				
0.35	80.1	80.0	79.9	79.8	79.8	79.7	79.6	79.5	79.5	79.4	79.3	79.3	86.0						
0.40	79.5	79.5	79.4	79.3	79.2	79.2	79.1	79.0	78.9	78.9	78.8	85.0							
0.45	79.0	78.9	78.8	78.7	78.7	78.6	78.5	78.5	78.4	78.3	84.0								
0.50	79.4	78.3	78.3	78.2	78.1	78.0	78.0	77.9	77.8	83.0									
0.55	80.6	77.8	77.7	77.6	77.6	77.5	77.4	77.3	82.0										
0.60	81.8	77.3	77.2	77.1	77.0	76.9	76.9	81.0											
0.65	83.0	76.7	76.6	76.6	76.5	76.4	80.0												
0.70	84.2	76.1	76.1	76.0	75.9	79.0													
0.75	85.4	76.8	75.5	75.5	78.0														
0.80	86.6	78.1	75.0	77.0															
0.85	87.8	79.3	76.0																
0.90	89.0	81.5																	
0.95	90.8																		

Table 3.7: Expected value *given* sample information (EV|SI) for Paloheimo-Fraser (pftags) across a range of prior distributions. Columns differ by the probability that the population is truly at the target, P(trueAT). Rows differ as the probability that true stat is above the target, P(trueHI). The remaining probability, P(trueLO), is defined as 1 minus the sum of P(trueAT) and P(trueHI). When prior state probabilities tend to equality (i.e., maximal uncertainty), the EV|SI is only a fraction of that for Downing reconstruction (Table 6).

P(trueHI)	P(trueAT)																		
	0.05	0.10	0.15	0.20	0.25	0.30	0.35	0.40	0.45	0.50	0.55	0.60	0.65	0.70	0.75	0.80	0.85	0.90	0.95
0.05	81.6	74.2	66.7	59.3	51.8	44.3	37.1	33.8	30.8	32.2	33.5	34.8	36.0	42.7	52.7	62.6	72.6	82.5	92.5
0.10	71.6	64.2	56.7	49.3	41.8	34.4	30.3	27.0	27.0	28.3	29.6	30.9	35.3	45.2	55.1	65.1	75.0	85.0	
0.15	61.7	54.2	46.8	39.3	31.9	26.8	23.5	21.9	23.2	24.4	25.8	27.7	37.7	47.7	57.6	67.6	77.5		
0.20	51.7	44.3	36.9	29.4	23.3	20.0	16.7	18.0	19.3	20.6	21.9	30.2	40.1	50.1	60.1	70.0			
0.25	41.8	34.3	26.9	20.7	16.5	13.2	12.8	14.1	15.5	16.8	22.7	32.6	42.6	52.6	62.5				
0.30	37.0	31.1	25.2	19.3	13.4	8.8	9.0	10.3	11.6	15.2	25.1	35.1	45.1	55.0					
0.35	35.6	29.8	23.9	18.0	12.0	10.4	9.1	7.8	7.8	17.7	27.6	37.5	47.5						
0.40	34.3	28.4	22.5	16.6	13.3	12.0	10.7	9.4	14.4	21.7	30.0	40.0							
0.45	32.9	27.1	21.2	16.2	14.9	13.6	12.3	14.9	22.2	29.6	36.9								
0.50	31.6	27.7	24.3	20.9	17.5	15.2	15.4	22.8	30.1	37.5									
0.55	36.0	32.7	29.3	25.8	22.4	19.0	23.5	30.7	38.1										
0.60	41.0	37.6	34.2	30.8	27.4	29.5	34.8	40.0											
0.65	46.0	42.5	39.1	35.7	35.5	40.8	46.0												
0.70	50.9	47.5	44.1	41.5	46.7	52.0													
0.75	55.8	52.4	49.1	52.7	58.0														
0.80	60.8	57.4	58.7	64.0															
0.85	65.8	65.1	70.0																
0.90	75.1	80.0																	
0.95	90.0																		

Table 3.8: Expected value *given* sample information (EV|SI) for SPR (spr25_tags) across a range of prior distributions. Columns differ by the probability that the population is truly at the target, P(trueAT). Rows differ as the probability that true stat is above the target, P(trueHI). The remaining probability, P(trueLO), is defined as 1 minus the sum of P(trueAT) and P(trueHI). When prior state probabilities tend to equality (i.e., maximal uncertainty), the EV|SI is only half that for Downing reconstruction (Table 6).

P(trueHI)	P(trueAT)																		
	0.05	0.10	0.15	0.20	0.25	0.30	0.35	0.40	0.45	0.50	0.55	0.60	0.65	0.70	0.75	0.80	0.85	0.90	0.95
0.05	83.5	76.0	70.1	64.1	58.2	52.2	49.9	50.4	50.8	51.3	51.7	52.2	52.6	53.1	53.5	62.5	72.5	82.5	92.5
0.10	80.7	73.1	65.5	57.8	50.2	44.3	44.7	45.2	45.6	46.0	46.5	47.0	47.4	47.9	55.0	65.0	75.0	85.0	
0.15	78.0	70.3	62.7	55.0	47.3	42.7	41.4	40.1	40.4	40.8	41.3	41.7	42.2	47.5	57.5	67.5	77.5		
0.20	75.1	67.5	59.8	52.2	44.6	42.7	41.5	40.2	39.0	37.7	36.5	36.5	40.0	50.0	60.0	70.0			
0.25	72.3	64.7	57.1	49.4	44.0	42.8	41.5	40.3	39.0	37.8	36.5	36.5	44.8	53.1	62.5				
0.30	69.5	61.9	54.2	46.6	44.1	42.8	41.5	40.3	39.0	37.8	36.6	44.2	52.6	60.8					
0.35	66.8	59.1	51.5	45.3	44.1	42.9	41.6	40.3	39.1	37.9	43.7	52.0	60.3						
0.40	63.9	56.3	48.6	45.4	44.2	42.9	41.6	40.4	39.2	43.2	51.5	59.8							
0.45	61.2	53.5	46.7	45.5	44.2	42.9	41.7	40.4	42.7	51.0	59.3								
0.50	58.3	50.7	46.7	45.5	44.3	43.0	41.7	42.1	50.4	58.8									
0.55	56.3	50.6	46.8	45.5	44.3	43.0	41.8	49.9	58.2										
0.60	59.4	53.7	48.0	45.6	44.3	43.1	49.4	57.7											
0.65	62.5	56.8	51.1	45.7	44.4	48.9	57.2												
0.70	65.6	59.9	54.1	48.4	48.4	56.6													
0.75	68.7	63.0	57.2	53.6	57.4														
0.80	71.9	66.1	60.6	64.4															
0.85	74.9	69.2	71.4																
0.90	78.0	80.0																	
0.95	90.0																		

Table 3.9: Payoff matrices examined during sensitivity analysis. In the left column, the matrices are expressed in their original scales. In the right column, the scores are normalized to each matrix' range of payoff values. a) "risk averse" matrix used in the basic analysis; b) "strict" only rewards the correct decision; c) "posneg" mixes positive and negative payoffs but with lesser range than the risk averse matrix; d) "slight" differences between among payoffs and unique values in each cell; e) "slight2" has relatively slight difference across most of the matrix; f) "slight3" has even more slight difference across most of the matrix.

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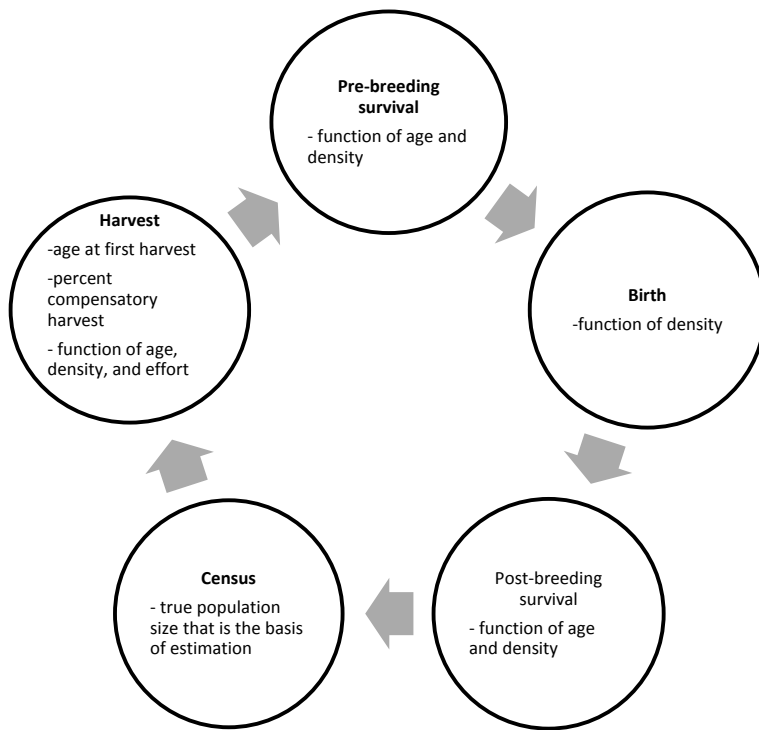


Figure 3.1: Annual cycle of events in the population as simulated using popMod.

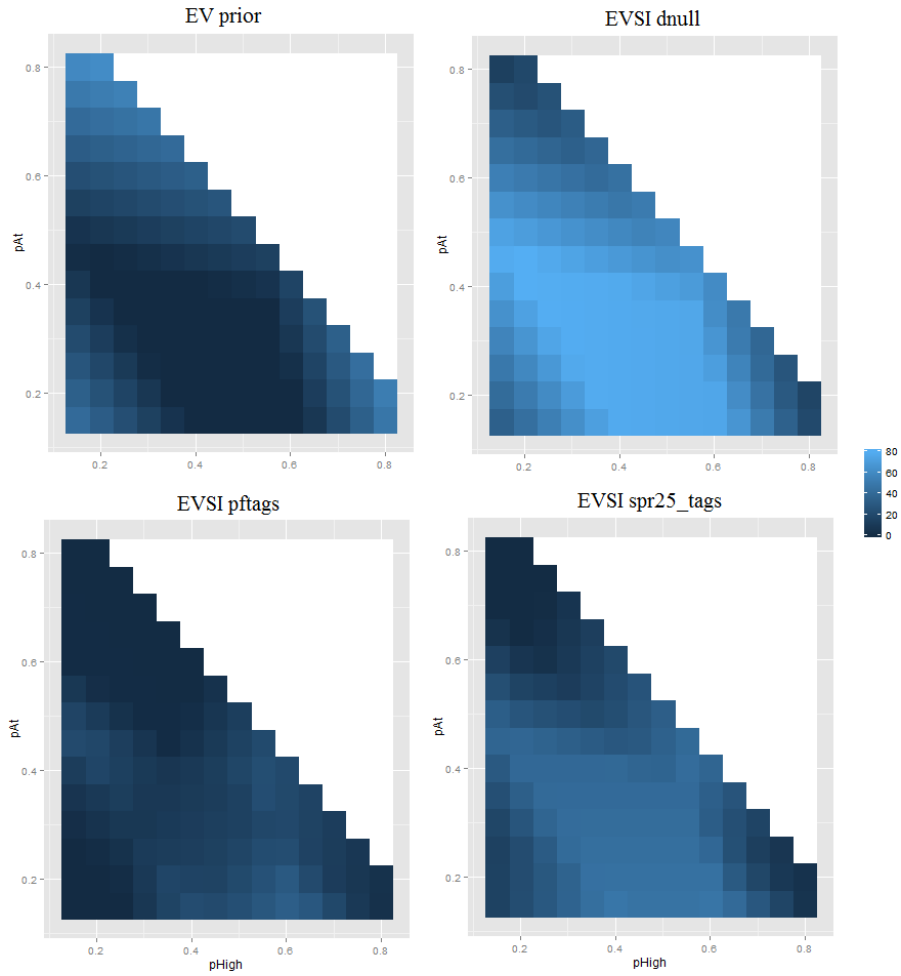


Figure 3.2: Expected values under a range of prior distributions. Lighter colors indicate higher values: a) expected value with only prior information (EV_{prior}), b) EVSI using Downing reconstruction, c) EVSI using Paloheimo-Fraser, and d) EVSI using SPR. Note that the EVSI values for each estimation strategy are the values of $EV|SI$ minus the EV_{prior} (chart a). EV_{prior} and $EV|SI$ values are also shown in Tables 3.6-3.8.

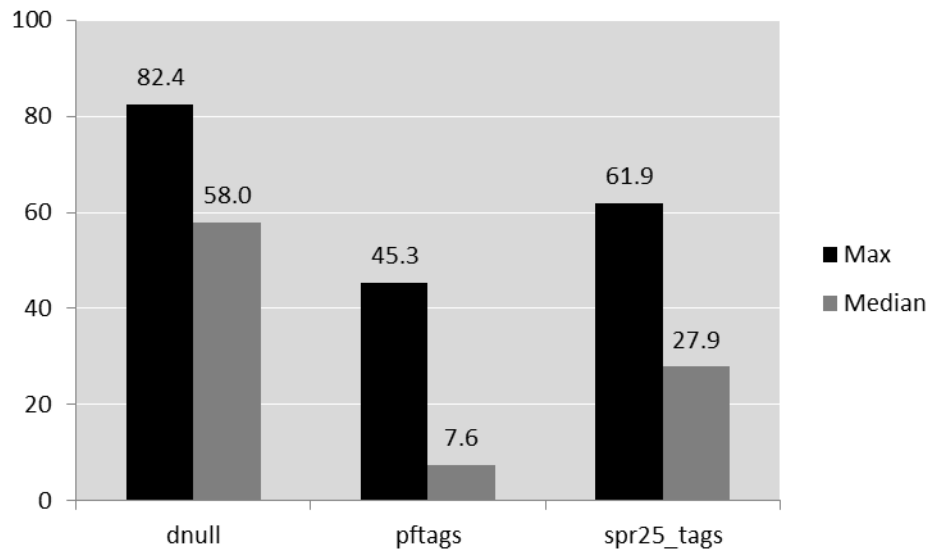


Figure 3.3: Maximum and median EVSI for three representative strategies. Statistics calculated across 190 different prior state distributions.

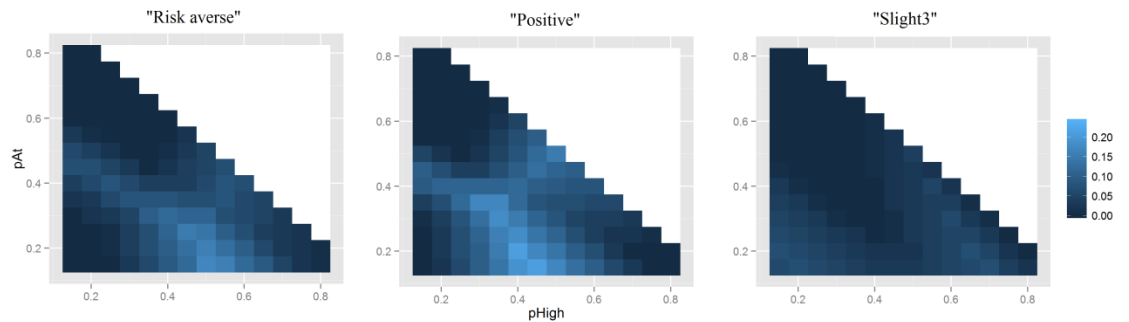


Figure 3.4: EVSI matrices for the pftags model under "risk averse" (left), "positive" (middle), and "slight3" (right) payoff matrices (Table 3.9). The range of EVSI scores is influenced by the range of payoffs in the matrix. The payoffs have been normalized to a 0 – 1 scale to facilitate direct comparison. Cell values in the figures correspond to different distributions of prior beliefs.

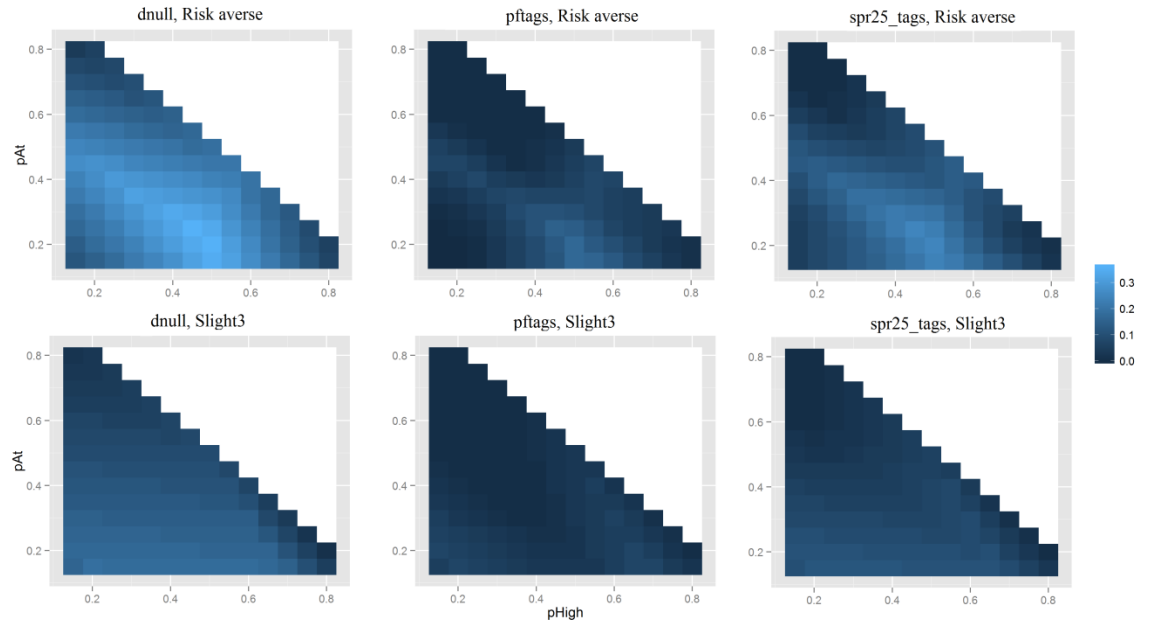


Figure 3.5: EVSI scores for dnull, pftags, and spr25_tags estimation strategies using the risk averse payoffs (top row) and the "slight3" payoffs (bottom row). Dnull has the most certain conditional probabilities and pftags, the most uncertain and EVSI values are proportional to the certainty of the sample information. These payoff matrices have been normalized to a 0 – 1 scale to facilitate direct comparison.

Chapter 4 Rigorous Opinions: A Hybrid Framework for Modeling

Expert Opinion and Hard Data

Abstract Habitat models are critical to anticipating and assessing the impacts of environmental changes and human development on wildlife habitat (Guisan and Zimmermann 2000, Nielsen et al. 2010, Bird et al. 2011, Jackson et al. 2011). Habitat modeling efforts are typically hampered by a paucity of hard data and model uncertainty in expert-based models (e.g. HSI models). We modeled habitat suitability for American black bears in Vermont, USA, by combining the information from expert opinion and empirical animal locations. We first obtained a map of habitat suitability in Vermont based on expert opinion. We then fitted a statistical model to this map, estimating the effects of a suite of covariates on habitat suitability. These estimates then became our prior effect distributions for a second analysis in which we validated and updated our model through Bayesian analysis of an independent animal location dataset. We examined the effects of different interpretations of the expert map (e.g. “primary” vs. “secondary” habitat) on the final results and compared them to a model fitted solely to the validation data (uninformative priors). Our modeling framework was robust to different interpretations of the expert map, with parameter estimates and fitted habitat suitability values being essentially identical after updating with the validation data. Statistical fit and the point estimates and precision of effects were much better for the analysis using prior information from the expert map than for the analysis with uninformative priors. Our final, fitted results represent an integration of expert opinion and empirical data that exist in a form that can continue to “learn” as new data become

available. It enables direct quantification of habitat suitability across broad regions and provides a rigorous description of the uncertainty inherent in that valuation. Quantifying uncertainty is a critical feature of decision-making that is generally absent from broad-scale habitat modeling efforts.

Keywords Bayes, expert opinion, habitat suitability, HSI, occupancy, *Ursus americanus*.

Introduction

Habitat loss and degradation threaten the persistence of wildlife species worldwide (Wilcove et al. 1998, Brashares et al. 2001, Schipper et al. 2008), and habitat conservation often depends on decisions based on proper valuation of affected habitat. Habitat models are critical to anticipating and assessing the impacts of environmental changes and human development on wildlife habitat (Guisan and Zimmermann 2000, Nielsen et al. 2010, Bird et al. 2011, Jackson et al. 2011). Frequently, adequate species-habitat data for statistical modeling do not exist. In the absence of empirical data, models must be built from expert opinion. Habitat Suitability Index (HSI) models (USFWS 1980, 1981) are theoretical, deductive models that comprise input variables (e.g., distance to roads, percent of habitat in the surrounding area), suitability functions for each variable (e.g., linear equations that specify the change in suitability as input variable changes), and an aggregating scheme for combining the individual suitability indices into a single HSI value per spatial unit.

HSI model development is fraught with challenges. One difficulty is that of translating perceptions of species distribution or habitat value into model parameter values. Using elicited opinion, habitat suitability model-building entails iterative calibration and verification to adjust parameter functions and ensure satisfactory and meaningful output (Brooks 1997). Another challenge is that the model structure and parameterizations are typically elicited from one or more experts, and discrepancy between experts' judgments can be the dominant source of uncertainty (Czembor et al. 2011). Because different models result in different predictions (Elith et al. 2006) and different conservation outcomes (Wilson et al. 2005, Hauser et al. 2007), it is important to assess the credibility of alternative models.

Yet another challenge with using HSI models is validating and updating them with empirical data as they become available (Roloff and Kernohan 1999, Mitchell et al. 2002). Depending on the species of interest, empirical data for validation may or may not exist across all or much of the area to which the HSI is applied (pers. comm. B. DeLeuca, UMASS Landscape Ecology Lab). The growing impetus for conservation planning that includes future uncertainty and variability carries with it the need to model systems and drivers at broad spatial scales (e.g., Rowland et al. 2014). Habitat mapping at broad scales requires striking a balance between expert opinion and empirical validation. Hard data may be limited to only portions of the region and could be used for localized, spatially-explicit validation. There is currently no rigorous mechanism for incorporating the new empirical information into the parameters of an expert model and doing so in pieces across a modeling expanse.

Despite these challenges, the use of expert opinion is common in wildlife habitat studies as there is a strong need to represent habitat values where empirical data do not exist. Bayesian models are a natural and increasingly favored means of combining expert and empirical information, typically with experts forming prior distributions for the analysis of limited empirical data (Yamada et al. 2003, Martin et al. 2005, Denham and Mengersen 2007, Griffiths et al. 2007, Mac Nally 2007, O'Neill et al. 2008, Murray et al. 2009 and James et al. 2010). The experts can help identify prior parameter distributions which can later be updated with empirical data. Elicitation is a tricky issue (Low Choy, et al. 2009), and experts may be better able to think in terms of discrete locations than abstract or mathematical relationships (Denholm and Mengersen 2007, James et al 2010). James et al (2010) developed a software tool for eliciting for model components from experts in a graphical context that provide visual feedback and allows experts to think in terms of discrete places rather. Once the initial elicitation is complete, the Bayesian analysis provides a seamless means of updating the model with additional data.

Here, we present a multi-step method for translating expert opinion into a statistical model of habitat suitability, and updating the result with independent empirical information. The approach begins with a graphical depiction (map) of expert opinion regarding the disposition of suitable and unsuitable habitat. We then analyze the map as the response variable of a Bayesian logistic regression with naïve priors, fitting it to a suite of environmental covariates. As new occurrence information becomes available, Bayes' Theorem is used to update the model parameters ("betas"), weighted geographically according to the empirical data's sample space. In this way, the HSI

model becomes a “living” model, spatially updated as new information accrues, and resting on expert opinion for locations within the region where data are sparse.

We illustrate this approach by analyzing black bear occurrence across Vermont, USA and using two separate empirical datasets to make spatially-explicit updates of the initial model based on expert opinion. Our objectives for this study were to 1) fit statistical models to maps of relative habitat quality for black bears across the state of Vermont as determined by knowledgeable experts: and 2) update the resulting models with independent, empirical animal location dataset.

Materials and Methods

Study Area

Vermont is predominantly covered by Northern Hardwoods forests dominated by Sugar Maple (*Acer saccharum*), Yellow Birch (*Betula allegheniensis*), Paper Birch (*B. papyrifera*), and American Beech (*Fagus grandifolia*). Elevation ranges from 30 meters (m) along the shores of Lake Champlain to 1339 m at Mount Mansfield. Mean January temperatures ranged from -10 °C to -5.5 °C, and mean July temperatures from 17.7 °C to 21 °C (Thompson and Sorenson 2000). Annual precipitation ranged from about 75 centimeters (cm) in the Champlain Valley to more than 180 cm along the southern Green Mountain peaks (Thompson and Sorenson 2000).

Human population density varied from extremely rural areas the northeast with 3.7 people per km², to the Champlain Valley, with 24% of the state’s population and a

human density of 91 people per km² (U.S. Census Bureau 2001). Although mostly rural, the population of Vermont has grown at least 10% per decade since the 1960s (U.S. Census Bureau 2001). Road density varies considerably from an average of about 0.53 km/ km² in Essex County to over 1.55 km/ km² in Chittenden County.

Study Species

Black Bears are large-bodied, generalist omnivores. They are long-lived and relatively slow to reproduce given delayed female primiparity, small litters, and biennial reproduction (Pelton 2003). Their diet consists mostly of vegetation and they hibernate in winter (Tøien et al. 2011). Bears must consume adequate nutrition in the warmer months to survive hibernation and to support reproduction. Late summer and fall are the critical feeding periods and bears can gain up to a kilogram of mass per day when food is abundant (Jonkel and Cowan 1971). Bears, especially males, may move often and range widely in search of food during late summer and fall, contributing to the greater vulnerability of male than female bears to fall hunting (Pelton 2003). Females are also less vulnerable to fall harvests because they den first, followed by sub-adults, and finally adult males (Jonkel and Cowan 1971, Johnson and Pelton 1980, Schooley et al. 1994). In the northeastern USA and Eastern Canada, denning occurs from September-November to March-May.

Distribution of food and heavy cover providing refuge from human activity are generally recognized as primary components of prime bear habitat (Rogers and Allen 1987, Clark et al. 1993, Mitchell et al. 2002, Pelton 2003). Black bears readily habituate

to living alongside humans (Pelton 2003), but proximity to humans also increases mortality risks to bears through legal, illegal, and accidental means (Rogers and Allen 1987, Rogers 1989, Mattson 1990).

Objective 1: Fit statistical model to a binary map of suitable-unsuitable habitat

The Vermont Fish and Wildlife Department possesses a map of putative bear habitat that is derived from decades of experience of multiple biologists with reference to information on bear harvest, sightings, conflicts, road kills, and other information (F. Hammond, VT Fish and Wildlife Dept., pers. comm.). This map is a graphical compilation of expert opinion, a visual representation of the informal model of bear habitat suitability in Vermont. The map is divided into several categories of habitat quality ranging from the best to the worst. We digitized this map as a raster object (Figure 4.1) at 90m x 90m resolution with each cell bearing one of four habitat quality levels present in the original document: 1) primary habitat, 2) secondary habitat, 3) tertiary habitat, or 4) poor habitat.

We translated this map of ordinal categories into a binary map for the purposes of statistical estimation. For this study, we assumed that habitat suitability categories indexed probability of occupancy and that the proportion of area occupied, either across a spatial area or within some set of points, will be directly proportional to habitat suitability. We created two habitat value maps with different coding schemes to examine model sensitivity to this processing of the original inputs. The coding replaced the four habitat categories with values of 1 or 0, to create a binary dataset from which the

probability of occupancy could be estimated using logistic regression. This model form was desirable as it would also be amenable to the presence-absence data that we subsequently used for validation and updating of the initial model fit.

The first step was to assign ordinal values to the habitat classes. We assigned values of 1.0, 0.7, 0.5, and 0.2, in order from primary to poor habitat. These values can be interpreted as probabilities of occupancy and of habitat suitability where the most suitable habitat supports the densest and most persistent population densities and the poorest habitat can support bears but is expected to do so at lower densities. These habitat values were then recoded as binary values according to a classification threshold, a value on the 0-1 spectrum. Any habitat values above the threshold were interpreted as 1's and any values below were treated as 0. In the first case ("strict"), we chose a threshold between 0.7 and 1, encoding the primary habitat as 1 (0 – 1 scale) and all other habitat categories as 0. In the "inclusive" case, we encoded primary, secondary, and tertiary habitat as 1 (threshold between 0.5 and 0.2) and gave only the poorest habitat a value of 0.

For the first phase of analysis, we sought to identify correlations between the patterns of the expert map and measurable landscape-scale covariates. To do so, we overlaid 1000 sample points arranged, in a state-wide regular lattice, assigning a value of 1 or 0 at each sample point depending on the suitability score on which each fell. There was no constraint on the number of sample points (other than computing time), and we elected to use 1000 points with a resulting density of approximately 1 point per 25 km², the approximate average size of a female black bear home range. This was a small enough sample for quick computation but large enough that the uncertainty in the

resulting covariate effects resulted from uncertainty about the covariate associations and not from sampling variability.

We used National Land use - Landcover data (NLCD) to characterize ecological covariates of habitat quality. We first resampled the NLCD data from 30 x 30m to 90m x 90m resolution in a GIS using a majority rule. When there is no clear majority, the GIS algorithm assigns a value of “No Data” to the resulting cell. We filled any of the No Data results by also resampling the data to a 120 x 120 m resolution (which did not have any No Data results), subsampling back to the 90 x 90 m resolution and then using the results to fill any No Data cells in the original resampled layer. After resampling to the new resolution, we reclassified some of the NLCD data into thematic categories for use in our models: residential and developed classes (“res”); row crops, orchards, pastures and grassy open space (“agopen”); and forested and emergent wetlands (“wet”). We also used the three NLCD forest cover types: deciduous (“dec”), coniferous (“con”), and mixed (“mix”). To avoid collinearity, we calculated rank-order correlation coefficients between each pair of potential covariates in a random sample of cells ($n = 1000$) from the NLCD layer. We sought to avoid correlations less than -0.6 or greater than 0.6 between any two variables. The correlation was 0.68 between coniferous and mixed forest, so we combined these into a single category comprising coniferous and mixed forest types (“conmix”), which then met or conditions for inclusion in the model. No other correlations exceeded our criteria.

Each 90 x 90 raster cell across a map of Vermont was assigned the percentage of each land cover covariate found within a 990 x 990 m square moving window. To these

percentages of landcover covariates, we added “core” habitat blocks, the amount of area in contiguous areas of homogenous natural community types (e.g. forest) that are unbroken by roads, development or agriculture. We rasterized a polygon layer of contiguous habitat blocks, assigning each cell a value equivalent to the area in square kilometers of the contiguous block in which it occurred. Given the mobility of black bears, we ignored potential edge effects of these blocks. We assumed that a bear in any portion of such a block would be able to access the entire block.

For both the “strict” and “inclusive” expert inputs, we fit a Bayesian logistic regression to the expert data using R (R Core Team 2013), WinBUGS (Lunn et al. 2000), and the R package R2WinBUGS (Sturtz et al. 2005). We sampled a regular lattice of points from the expert map and the covariate data layers and fit them using Uniform (-10, 10) prior distributions for covariate effects. We compared parameter estimates and precision across types (“strict”, “inclusive”) of analysis using Receiver Operating Characteristic (ROC) curves. We used the area under the ROC curves (AUC) to compare the ability of the statistical models to “predict” the map from which it was estimated. The AUC is interpreted as the probability that a randomly chosen pixel from the expert map, if it has a value of 1, is classified higher than if the random pixel were actually a 0. A random classifier would have an AUC of 0.5 and greater AUC suggests better classification.

Objective 2: Update model with independent, empirical animal location dataset.

We used bear scat location data from Long et al. (2011) as an example of “new” empirical data that can be used to update the HSI models. The dataset comprised 162 sample sites from across the state that were sampled for bear presence using scat-sniffing dogs, camera traps, and hair snares in the summers of 2003 and 2004 (Long 2006, Long et al. 2011). Sites consisted of multiple transects that were all sampled during one to three visits over the course of the study. The majority of sites were visited once and subsets of sites were visited on two and three occasions. Trained dogs and dog-handlers detected fresh scats, identifying them to species in the field and collecting them for corroborative testing. Summer bear scats were visually distinctive and subsequent genetic testing confirmed species identification by dogs and handlers. Automatic cameras and hair-snares were also deployed at some sites. See Long et al. (2011) for a full discussion of the study and description and evaluation of the methods.

The analytical model for the scat detection data was a logistic regression for site occupancy with a joint model for detection probability to account for imperfect detectability. The covariates for detection were year of survey and method of detection (dog and other). The “updated” or “validated” model was the result of fitting this detection-occupancy model using the effect distributions estimated in the previous step as prior effects distributions for occupancy and Uniform (-10, 10) priors for the detection effects. We also fit this model using uninformative priors in order to examine the impact of the prior information on the results.

To simulate having data from multiple studies that could be used for iterative updates, we split the empirical data into northern and a southern datasets along a natural horizontal break between survey locations near the middle of the state. We treated the two datasets as distinct from one another, each with a study area that covered roughly half of the area over which the expert map was fit. After fitting the expert map, we performed two separate updates, one using the northern dataset and one using the southern. Finally, a map of the state was produced that combined the southern update and the northern update, each within their respective boundaries.

We fit the state-wide model by fitting predictions from the prior model across the entire region and then updated those areas represented by the validation data. To accomplish this, we generated a predicted surface for both updated models, and then created one single surface by taking the weighted sum of model predictions for each map pixel. We created a data layer with a model weight, w , between 0 and 1 for every cell in the region. This weight indicates the degree of membership of a given cell in the sample space of the northern validation study, hence the raster cells had weights of 1 in the north and 0 in the south. The proportion of weight given to the northern update of the model was w , and the weight for the southern update model was $1-w$. The weights allow each separate update to be featured within its study area and the two models grade into one another across a 20 km-wide band spanning their borders.

Results

Objective 1: Fit statistical model to a binary map of suitable-unsuitable habitat

Differences in beta estimates from different interpretations of the expert map (inclusive vs. strict) were apparent in the first posterior estimates (before updating with Long et al. data; Figure 4.2). The greatest difference in model betas was seen for the effect of residential and wetland cover. These effects also had the greatest uncertainty, so they were not estimated well from the data. Both are relatively sparse cover types in Vermont. Each covers less than 2.25% of the state. The effect size for the “core” habitat blocks was of small magnitude due to the scale of that covariate, but was very influential in the fitted results. This is as expected as the amount of unbroken habitat a characteristic strongly linked to black bear habitat quality in Vermont. By virtue of core habitat blocks the fitted map follows the pattern seen in the expert with the notable exception in the upper, middle portion of the state.

The models estimated from the two interpretations of priors are similar in appearance with the inclusive prior estimates leading to a map with more area falling in the upper quantiles of the HSI scale (

Figure 4.3). The “relief” of the two maps is similar, but the inclusive interpretation of the expert map looks like the strict map with cells shifted slightly upward in HSI value (i.e., darker), consistent with the expert map interpreted as having a greater amount of suitable area.

The maximum AUC for the posterior based on the strict model was 0.8 and the maximum for the inclusive posterior was 0.75. The optimal threshold for classification (threshold associated with highest AUC) for the strict model was 0.35 and that for the inclusive model was 0.5. Based on the AUC statistic, the strict interpretation of the expert map appeared to be the better fit and hereafter, we will discuss the updating of the strict-based model.

Objective 2: Update model with independent, empirical animal location dataset.

The first posterior map (estimated from the expert map) was updated using the two scat detection datasets. Each dataset was used to update the half of the map from which the data originated, while the rest of the map retained the pre-update, first posterior values. The resulting two updated models (**Error! Reference source not found.**) were then combined into one using the model weights layer (Figure 4.6).

The effects changed little for most of the covariates from the first model fitting to the update (Table 4.2; Figure 4.4). The clearest difference was in the amount of agricultural and open land in the northern vs. southern portions of the state. For the less common cover types (e.g. res, wet) and the widely and relatively-evenly distributed types (e.g. dec) the effects changed little in terms of the magnitude of the estimated effect or their precision.

All of the covariate values had positively-skewed distributions and landcover types other than deciduous and conifer-mixed forest were relatively rare (Table 4.1). The northern data area had more residential/developed landcover, more agriculture and open

landcover, and more wetland cover than the southern part of the state. All three of these classes were still rare, but in the north, there were more locations that had very high values, leading to a greater skew to the distributions. Large core habitat blocks are generally found along the Green Mountains and in the northeast corner of the state, resulting in greater values of the core covariate in the North.

Although development, agriculture, and wetlands are thought to have non-trivial impacts on black bear habitat quality, the data presented here had not strong signal, at least partly due to the relatively homogenous, forested character of Vermont and the coarse grain of the data and analysis.

Discussion

This habitat modeling effort was an attempt at using a simple, graphical representation of habitat quality as the basis for a fitted Bayesian model that could be updated with empirical data. Our proposed method addresses two key concerns in expert-based habitat modeling, elicitation of information and model validation. The expert map was built up over many years by biologists with the Vermont Fish and Wildlife Department, and we considered it to convey information that was not directly accessible with typical broad-scale GIS data. For that reason, we used the map itself as the expert opinion and sought to “train” statistical effects distributions from it directly. This then, formed the basis of the analysis of the empirical bear location data. Previous analysis of the bear scat dataset (Long, et al., 2012) resulted in a broadly-distributed, high probability of occupancy by black bears across Vermont. We attempted to bridge the spatially-

restricted expert assessment of range quality and the broadly-distributed empirical detections with an analytical framework that could borrow information from both sources and integrate it into a hybrid evaluation of habitat (Low Choy, et al. 2009).

Other authors have presented models that integrated opinion-based or synthetic models and empirical data as a means of validation. Recently, Kaminski, et al (2013) borrowed existing expert-based habitat suitability functions for black bears and supplemented them with field data collection to adapt the model to their specific study region. They borrowed from the work of Powell et al (1997) who used field data to estimate univariate relationships between black bear space use and habitat features and then combined many such models into a habitat suitability model for the Southern Appalachians. Once parameterized, the Southern Appalachian model was validated, once in its initial form, and again (Mitchell et al. 2002) after eliminating variables from the model that appeared unnecessary in the first validation. Alteration of that model, as with deletion of a variable by McLaughlin et al (1999) from the HSI model for black bears in Maine, was an ad hoc elimination of model elements that appeared superfluous upon validation.

Our method merely packages that same process into a statistical framework that can estimate effects, combine them into the HSI score, and “remove” unwarranted covariates by letting their values shrink to 0 as the evidence warrants. In this analysis, the effect of the “informed prior” estimated from the expert map was strong relative to the information in the empirical data. Different covariates could potentially tease out stronger patterns in the empirical data, but this is unlikely when limiting the analysis to remotely-

sensed data. However, different data did alter the relative influence of the prior versus the empirical update. We analyzed models at all stages of the process presented here using a variety of other covariates to in an attempt to find better-fitting models (unpublished analyses). In some cases, the expert map fit very poorly but the effects for the empirical data were strong (e.g. using a single NLCD “forest” category). In that case, the updating very clearly changed the effect estimates. Ultimately, using remotely-sensed data, we did not find any constellation of covariates that was strongly correlated with both the expert map and the empirical data. This could mean that the experts are truly encoding information that is absent from the empirical study or that the two data sources are simply too divergent in the underlying quantity they encode to blend well.

Assessing the fit of our logistic model of the expert map is a non-trivial challenge. We know that the ecological correlates and drivers of black bear habitat occupancy are not neatly bounded by the zones depicted in the expert map. The expert map identifies concentrations of certain conditions that are considered beneficial to black bears in Vermont and we attempted to use this as a guide in developing a statistical model that offered more flexibility of use. The abiotic and biotic elements of black bear habitat extend across and outside the designated polygons and we fully expected the resulting maps to lose the stark contrast of the expert map. However, by using the expert map, we hoped to capture the general pattern depicted, to train the statistical model in a manner consistent with existing knowledge but to put it in a flexible analytical form.

In our application, the resulting map was a much more diffuse map than the expert map, due mostly to the absence of covariates that clearly followed the distribution

indicated in the expert map. The dominant vegetation types and other variables were much more broadly distributed than the highest quality ranges. Furthermore, the empirical data did not exert a large influence on the model effect estimates. These same data have been used in a typical occupancy analysis that also resulted in imprecise effect estimates (Long, et al., 2012) essentially dominated by the generally positive effect of forest cover. The empirical data show bears occupying a wide range of forested locations and being broadly distributed in the state. The effect of this data on the model was to generally raise the habitat value across the state, especially in the north. This outcome highlights the value of being able to jointly model multiple sources of data. The empirical data are telling us to relax the expert model a little and allow that the habitat quality is relatively high across more of the state than the expert map suggests. At the same time, we were able to let the expert map largely shape the final outcome rather than let the state map be determined solely by the empirical study.

The practice of modeling habitat “quality” or “suitability” presents many challenges of definition as well as implementation. The range quality represented by the experts and the occupancy state inherent in the empirical data may not be closely-enough linked to allow their efficient combination. Occupancy may be a poor state to monitor for an abundant, wide-ranging species far from range frontiers. Low-quality habitat can be occupied, even by high population densities, based on individual movement and social and population dynamics (Charney 2012, Van Horne 1983, Garshelis 2000, Schmidt and Pellet 2005). Tyre, et al. (2001) demonstrate that habitat occupancy may be more indicative of the processes governing dispersal than those governing birth and death rates

as is often implied or assumed by notions of habitat quality. Yet these concerns are neither new, nor unique to this study. Proper care must be exercised in any modeling effort, regardless of the data or structural methods employed.

Conclusions

The methods presented here offer a potentially efficient and effective way to construct habitat suitability maps for broad areas when empirical data are sparse or lacking. The graphical representation of expert opinion simplifies the initial elicitation and allows the construction of a statistical model trained on the information provided. As a statistical model, it is then amenable to parameter updating through iterative validation. In the example resented here, we used expert opinion to formulate a base model across a large area. We then incorporated statistical updates of that base model for multiple, separate areas and combined them all into a single habitat model.

As in all expert-based model-building exercises, care must be taken to ensure common interpretations and definitions of quantities and processes. Nevertheless, discrepancies can occur when the experts infer an underlying reality that is difficult to sample empirically. In the case at hand, the scat-based detection of black bears does not identify timing or intensity of local habitat use. A single scat counts as much as a multitude. Alternatively, the expert focus on “backcountry” strongholds as primary bear habitat reflects a long-term view about species persistence that may be overly conservative. Or, this view could include not just assessments of habitat quality, but implicit management strategy or objectives that emphasize certain portions of the range

more than others even when suitability differs little. To the extent that both the expert map and the empirical data can teach us something, we need some way to integrate them into the management of the species. Having a model to do that may improve the interpretation of this information and allow it to be used directly and transparently in the planning and decision-making.

We believe that this model could be extended across wider areas to formulate regional models and has the added benefit of supporting computation of credible intervals for any and all cells on the map. The ability to estimate uncertainty may be as valuable as the point estimates. Our hope is that this flexible method facilitates a mosaicking of habitat models across regional landscapes in a dynamic and spatially-specific manner, resulting in locally realistic and constructive approximations of habitat value for the purposes of long-term conservation. The resulting models could also outlive any one creator or user and become a living model that is repeatedly updated with additional information as it becomes available.

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Figure 4.1: Expert approximation of black bear habitat suitability in the state of Vermont. Primary habitat coincides with low human activity and more continuous forest cover. Secondary and Tertiary habitat are well-forested areas but with higher levels of human residency and activity. The Poor habitat includes relatively high amounts of agricultural and open landcover types and the highest human residential densities.

Figure 4.2: Comparison of the prior effect estimates and 95% credible intervals between the “strict” (gray) and “inclusive” (black) interpretations of the expert map. RES and WET cover ~2.5% and ~1.5%, respectively, of the land area in Vermont.

Figure 4.3: The expert (upper) and first posterior (lower) models fit to the state of Vermont. The maps on the left are the “inclusive” interpretation of the expert map and those on the right follow the “strict” interpretation.

Figure 4.4: Estimated covariate effects (dots) and 95% credible intervals (bars) of the first posterior (black), Northern update (medium gray), and Southern update (light gray). The study areas appeared to differ most clearly in the amount of agricultural and open land (agopen). Points are offset vertically to avoid over-plotting.

Figure 4.5: The updated maps based on data from the northern (left) and southern (right) halves of the state. Updates are applied in the half of the state where the data originated. The remainder of the map is the non-updated fit of the first posterior model estimated from the expert map.

Figure 4.6: The model-averaged state-wide habitat map.

Table 4.1: Summaries of the distributions of covariate values between the Northern and Southern study areas.

Northern						
	RES	AGOPEN	DEC	CONMIX	WET	CORE
Minimum	0.000	0.000	0.000	0.000	0.000	0
1st Quart	0.000	0.000	0.080	0.080	0.000	3
Median	0.000	0.000	0.140	0.245	0.000	20
Mean	0.015	0.100	0.137	0.295	0.017	102
3rd Quart	0.010	0.020	0.190	0.490	0.000	140
Maximum	0.360	1.000	0.310	0.860	0.500	626

Southern						
	RES	AGOPEN	DEC	CONMIX	WET	CORE
Minimum	0.000	0.000	0.000	0.000	0.000	0
1st Quart	0.000	0.000	0.088	0.118	0.000	17
Median	0.000	0.000	0.160	0.245	0.000	48
Mean	0.006	0.037	0.167	0.282	0.008	118
3rd Quart	0.000	0.000	0.230	0.440	0.000	206
Maximum	0.070	0.590	0.420	0.880	0.120	364

Table 4.2: Covariate effect estimates based on the strict expert map

	First Posterior		SOUTHERN		NORTHERN	
	mean	sd	mean	sd	mean	sd
Intercept	-0.80	0.23	-0.54	0.20	-0.31	0.20
res	-6.11	1.79	-6.08	1.78	-6.23	1.71
agopen	-1.35	0.54	-1.12	0.52	-0.35	0.47
dec	-0.07	0.99	0.30	0.92	0.63	0.93
conmix	1.06	0.38	1.18	0.36	1.22	0.36
wetscrub	-4.80	1.81	-4.67	1.83	-3.65	1.76
core	0.02	0.00	0.02	0.00	0.02	0.00

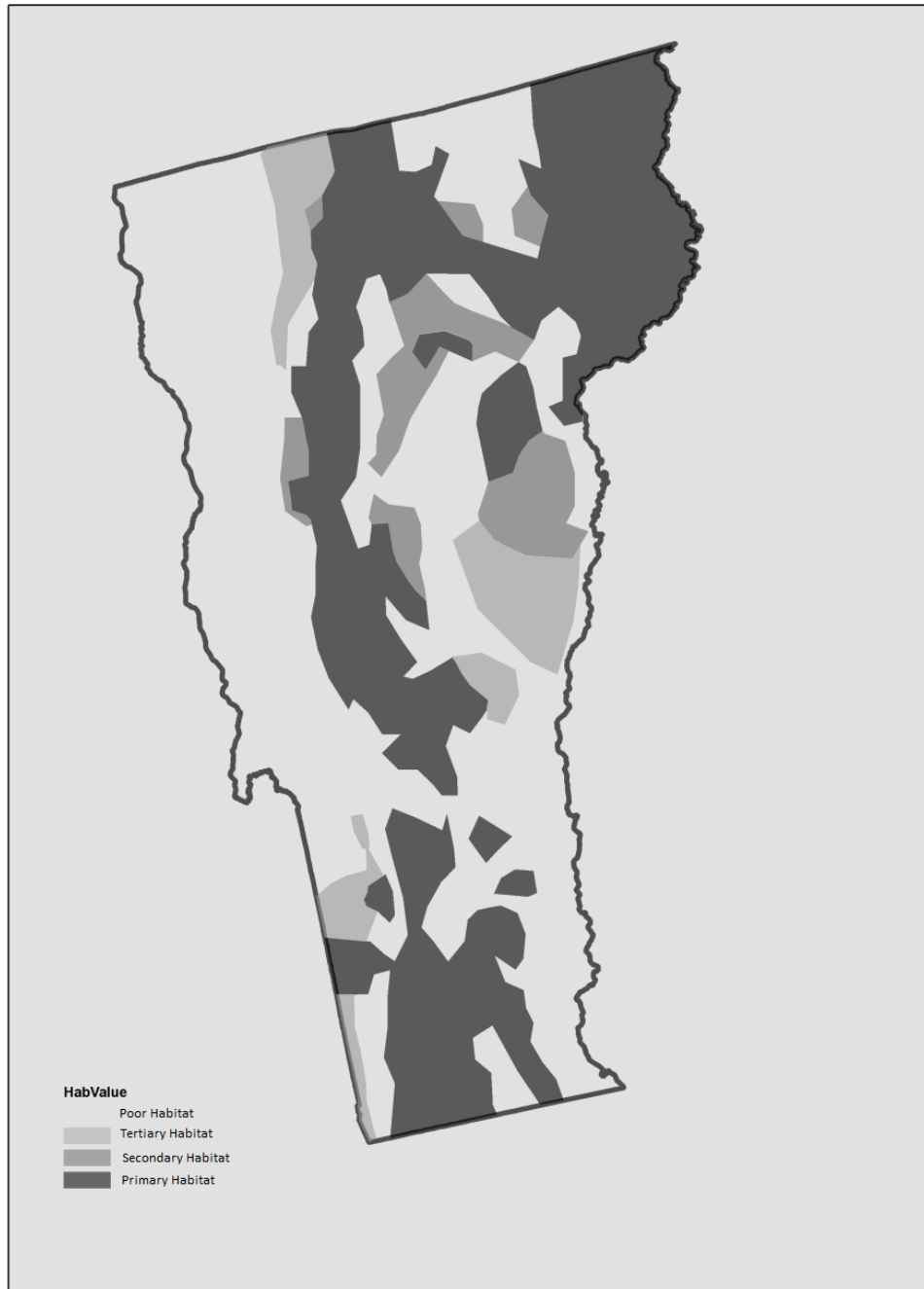


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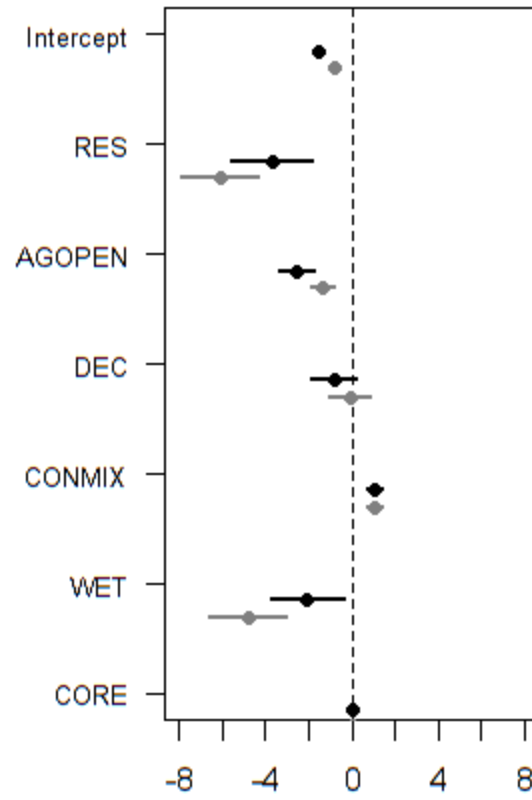


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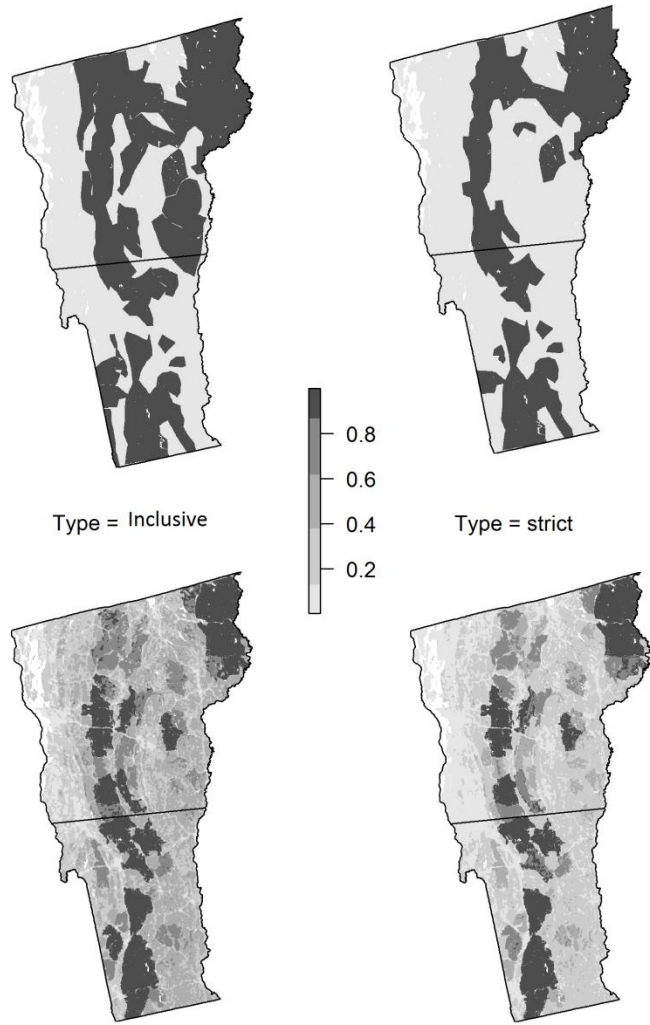


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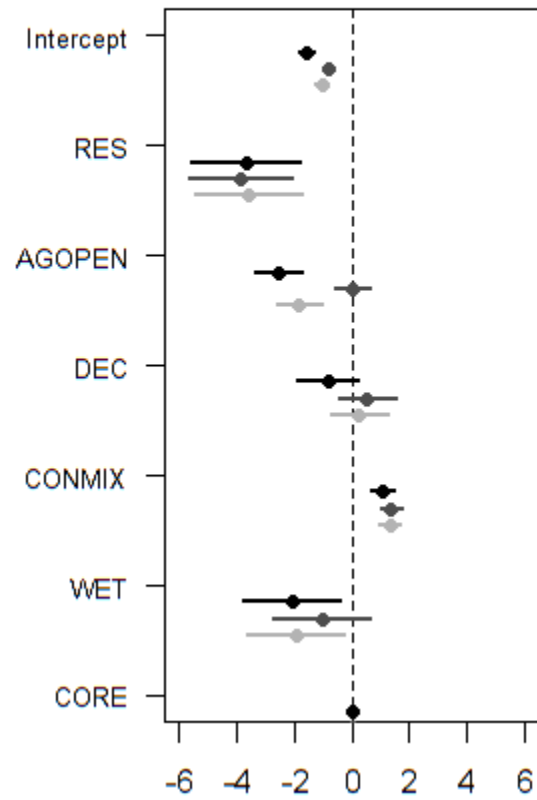


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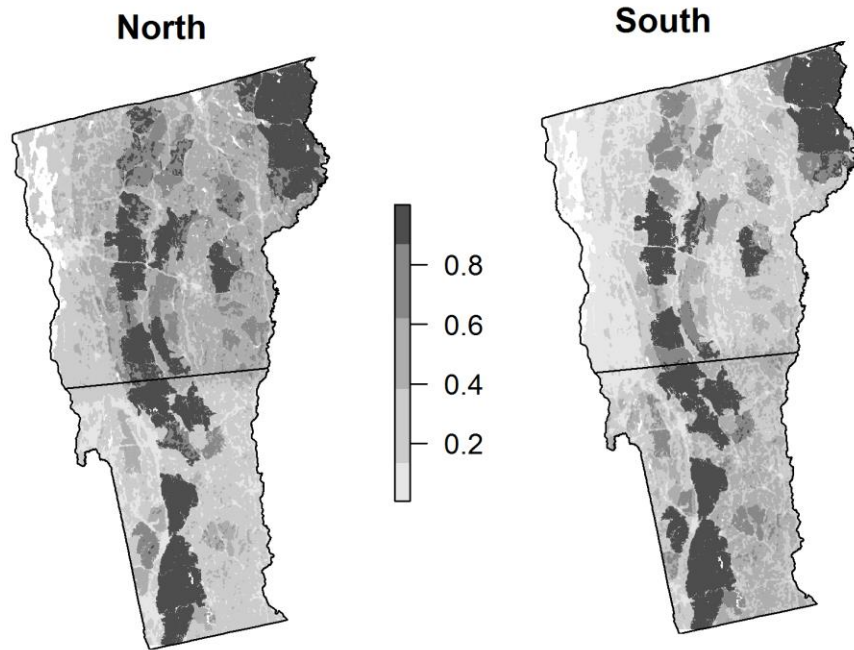


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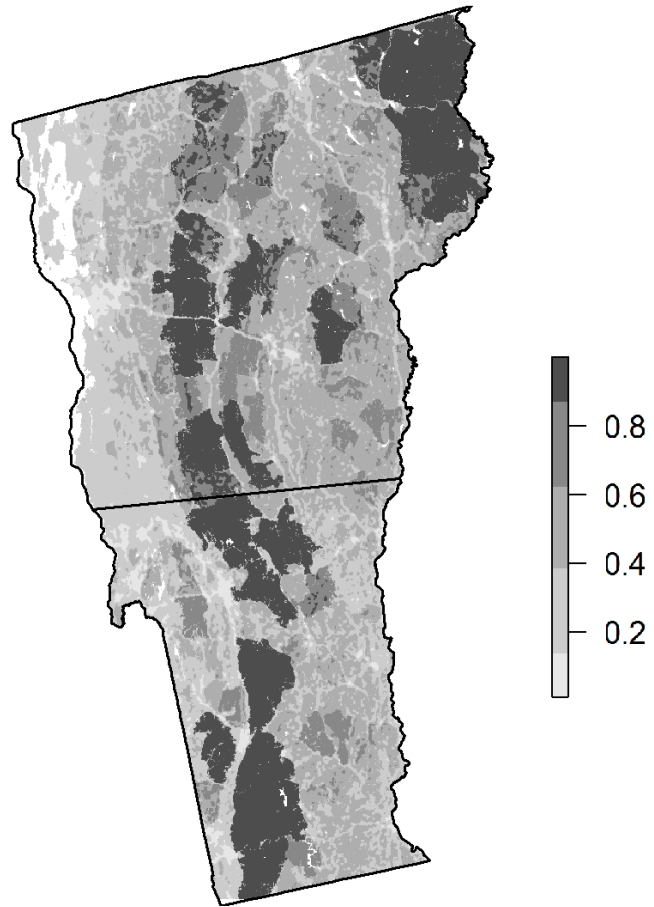


Figure 4.6: The model-averaged state-wide habitat map.

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