

Costs of detection bias in index-based population monitoring

C. T. Moore & W. L. Kendall

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Abstract

Costs of detection bias in index-based population monitoring.— Managers of wildlife populations commonly rely on indirect, count-based measures of the population in making decisions regarding conservation, harvest, or control. The main appeal in the use of such counts is their low material expense compared to methods that directly measure the population. However, their correct use rests on the rarely-tested but often-assumed premise that they proportionately reflect population size, i.e., that they constitute a population *index*. This study investigates forest management for the endangered Red-cockaded Woodpecker (*Picoides borealis*) and the Wood Thrush (*Hylocichla mustelina*) at the Piedmont National Wildlife Refuge in central Georgia, U.S.A. Optimal decision policies for a joint species objective were derived for two alternative models of Wood Thrush population dynamics. Policies were simulated under scenarios of unbiasedness, consistent negative bias, and habitat-dependent negative bias in observed Wood Thrush densities. Differences in simulation outcomes between biased and unbiased detection scenarios indicated the expected loss in resource objectives (here, forest habitat and birds) through decision-making based on biased population counts. Given the models and objective function used in our analysis, expected losses were as great as 11%, a degree of loss perhaps not trivial for applications such as endangered species management. Our analysis demonstrates that costs of uncertainty about the relationship between the population and its observation can be measured in units of the resource, costs which may offset apparent savings achieved by collecting uncorrected population counts.

Key words: Wildlife surveys, Detection bias, Opportunity costs, Optimization, Uncertainty, Decision making.

Resumen

Costes de los sesgos de detección en el monitoreo de poblaciones basado en índices.— Los gestores de poblaciones de fauna silvestre a menudo toman decisiones relativas a la conservación, recolección o control a partir de medidas indirectas de la población basadas en recuentos. El principal atractivo que presenta este tipo de recuentos son los bajos costes de material, en comparación con otros métodos que miden la población de forma directa. Sin embargo, el correcto uso de los mismos depende de una premisa que suele darse por sentada, aunque rara vez se comprueba, y que consiste en suponer que reflejan proporcionalmente el tamaño de la población; es decir, que constituyen un índice poblacional. El presente estudio investiga la gestión forestal de dos especies en peligro de extinción: el pájaro carpintero de cresta roja (*Picoides borealis*) y el zorzal mustelino (*Hylocichla mustelina*) en la Reserva Nacional de Animales Salvajes de Piedmont, en Georgia central, Estados Unidos. Se simularon varias políticas de conservación bajo escenarios referentes a las densidades del zorzal mustelino insesgados, con un consistente sesgo negativo y con un sesgo negativo dependiente del hábitat. Las diferencias obtenidas con respecto a los resultados de simulación entre los escenarios de detección sesgados y los no sesgados indicaron la pérdida prevista en los objetivos en materia de recursos (en este caso, el hábitat y las aves del bosque) a través de una toma de decisiones basada en los recuentos poblacionales sesgados. Teniendo en cuenta los modelos y la función de los objetivos que hemos empleado en nuestro análisis, las pérdidas previstas ascendieron al 11%, lo que supone un porcentaje bastante significativo en aplicaciones tales como la gestión de especies en peligro de extinción. Nuestro análisis demuestra que los costes de incertidumbre

acerca de la relación entre la población y su observación pueden medirse en unidades del recurso dado; es posible que estos costes compensen los ahorros aparentemente conseguidos mediante la recopilación de recuentos poblacionales no corregidos.

Palabras clave: Estudios de fauna silvestre, Sesgos de detección, Costes de oportunidad, Optimización, Incertidumbre, Toma de decisiones.

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Introduction

Managers of animal populations and wildlife habitats often rely on indirect measures of population abundance to support decision making in conservation, harvest, or control. For example, conservation decisions made by an agency may be based on numbers of singing birds detected during a roadside survey rather than on a direct estimate of population abundance. The use of such count-based measures is common because they are popularly perceived to be substantially less expensive to collect than data that allow the direct estimation of population abundance, while almost as informative.

But this perception is frequently unfounded. Ancillary data that permit direct estimation of abundance (or density) often can be collected at marginal additional expense to that of the original survey (Anderson, 2003): counts by paired observers (Nichols et al., 2000) and distances to subjects (Buckland et al., 2001) are two of many types of such data sources (Williams et al., 2002). More importantly, the fact that bias in the count (as a measure of population status) is almost never quantified renders its information content questionable (Anderson, 2001, 2003). The use of an unadjusted count as a measure of relative population abundance is valid only if the measure is strictly proportional to population size. In other words, the expected detection rate of the population (i.e., average of count / population) must remain constant over all conditions for the count to constitute a valid index (Anderson, 2001; Williams et al., 2002). However, this assumption is rarely tested in practice, and where it has been tested, detection rate is often found to vary (Williams et al., 2002). Factors associated with variation in detection rate include habitat features, environmental conditions, sampling and observer characteristics, and population abundance itself (Verner, 1985; Anderson, 2001).

In conservation decision making, one possible consequence of using counts unadjusted for detection rate is that decisions that appear best (i.e., optimal for some objective outcome) on the basis of such counts may not be the same as those that would have been chosen had true abundance been known or estimated. Therefore, an opportunity cost, measurable in units of the resource, may be associated with the use of unadjusted count data. The opportunity cost could be commensurate with, or even greater than, the cost of obtaining the ancillary measurements to permit direct abundance estimation. For some problems in wildlife conservation, for example, endangered species recovery, opportunity costs may not be inconsequential. Thus, the total cost of a monitoring program is equal to the cost of collecting the unadjusted counts plus the expected opportunity cost of either failing to estimate detection probability or establishing its constancy. If opportunity costs can be shown to be small over a range of plausible departures from the constant detection probability assumption, then the collection of unadjusted counts may be justified as

more efficient than alternative approaches.

Our study analyzes this problem in the context of forest management on the Piedmont National Wildlife Refuge (PNWR) in central Georgia (U.S.A.). Here, the joint objective of management is provision of habitat for an endangered species, the Red-cockaded Woodpecker (*Picoides borealis*), and the maintenance of a population of a shrub-nesting neotropical migratory bird, the Wood Thrush (*Hylocichla mustelina*). However, response of the Wood Thrush population to silvicultural actions is largely unknown, therefore the degree to which management for the woodpecker conflicts with management for the Wood Thrush is uncertain. We built a dynamic optimization model in which we specifically addressed this form of structural uncertainty. We also addressed uncertainty in the constancy of Wood Thrush detection rate among habitats. Simulating the decision making process under alternative forms of the optimization model yields a statistic, the expected value of information, that represents the opportunity cost of management under population measurement uncertainty. Although the models we will describe lack certain details that would make them useful in a management application, they are sufficiently useful for the purpose of illustrating the idea that real management costs may be incurred whenever there is considerable uncertainty about what an unadjusted population count is measuring.

Methods

Study area and description of management

The PNWR is a 14,136-ha unit of the U.S. National Wildlife Refuge System. The site supports a second-growth mixed pine (*Pinus taeda*, *P. echinata*) and hardwood (*Quercus* spp., *Carya* spp.) forest that regenerated naturally on severely eroded farmland abandoned in the 1930s (Gabrielson, 1943; Czuhai & Cushwa, 1968). Forest management is directed towards the maintenance of all native flora and fauna, sustenance of important ecosystems, and provision of public recreation, including wildlife viewing and sport harvest of some wildlife species (U.S. Fish and Wildlife Service, Piedmont National Wildlife Refuge, URL: <http://piedmont.fws.gov>). PNWR is also a designated recovery site for the Red-cockaded Woodpecker (U.S. Fish and Wildlife Service, 2000). The woodpecker's preferred foraging and breeding habitat consists of pure, open stands of mature (80 or more years) pine with a fire-maintained herbaceous understory (Loeb et al., 1992). But these forest habitats have become highly fragmented or have disappeared altogether, particularly since the early 20th century, as intensification of management on industrial forest lands emphasized shorter timber rotations and as exclusion of fire from all forest lands permitted increased hardwood succession (Ligon et al., 1986). Because the PNWR is identified as a woodpecker recovery site, forest

management is oriented towards increasing the abundance of this species. To this end, forest managers conduct aggressive regimes of thinning and regeneration cutting, prescribed burning, and mechanical vegetation removal to promote the creation of pure, open stands of mature pine with a herbaceous understory and reduced hardwood midstory (U.S. Fish and Wildlife Service, Piedmont National Wildlife Refuge, Habitat Management Plan, 1982; unpublished report).

Whereas these conditions are most favorable for production and survival of woodpeckers, their suitability for other forest wildlife species is mostly unknown. In particular, reductions in the hardwood midstory and the overstory canopy would be expected to be detrimental to the persistence of the Wood Thrush, a neotropical migrant species commonly associated with dense understory and midstory conditions of closed-canopy forest interiors (Weaver, 1949; Hamel et al., 1982; Roth et al., 1996). This species of management concern (Hunter et al., 1992) is thought to be declining over its range (Peterjohn et al., 1995), with fragmentation of interior forest conditions across the eastern U.S. implicated (Whitcomb et al., 1981; Temple & Cary, 1988; Hansen & Urban, 1992). Therefore, a concern for refuge managers is that silvicultural actions targeted for the woodpecker do not cause excessive harm to populations of nontarget species such as the Wood Thrush.

Comparison of Wood Thrush population parameters on control and silviculturally-treated forest compartments, both pre- and post-treatment, found no detectable effect of treatments on population growth of the Wood Thrush at PNWR (Powell, 1998; Powell et al., 2000). In fact, point estimates of many parameters and of the population growth rate were greater following treatments than before (Powell, 1998). However, parameter estimates had considerable sampling variability, therefore definitive conclusion of a treatment effect remains somewhat equivocal (Powell et al., 2000).

Decision model

We linked a model of annual Wood Thrush population dynamics to a forest management model, where both models were deterministic. The forest model expressed the quantities of and transitions among three PNWR forest seral types: pine regeneration (F1, age 0–20), mature mixed pine-hardwood (F2, age 20–90), and open pine forest suitable for woodpecker utilization (F3, age 20–90). Although pine habitat younger than approximately age 40 is seldom used by foraging woodpeckers (Epting et al., 1995) and age 16 is considered the transition point between the regeneration class and the poletimber (mature) class, our use of these assumptions greatly simplified the model and did not diminish its instructional value. At any time t , the proportional amounts of forest in each seral type was indicated in the vector

$$\mathbf{f}_t = [X_{F_1}(t), X_{F_2}(t), X_{F_3}(t)]'$$

In the absence of forest management, annual rates of natural transition from the mature classes into the regeneration class were $\tau_{12} = \tau_{13} = 1/70$, merely the inverse of the length of the mature age class (fig. 1A). Similarly, the graduation rate from the 20-year regeneration class to the F2 class was $\tau_{21} = 1/20$. When unmanaged, F3 forest can become unsuitable for woodpecker use in as few as 4 years (Piedmont National Wildlife Refuge, 1982, unpublished report), therefore, we assumed that F3 forest is lost at the rate of $\tau_{23} = 1/4$ per year in the absence of management.

However, management can cause regeneration to exceed the natural rates (through regeneration cutting), can effect the transfer of forest from the F2 class into the F3 class (thinning and burning), and can reduce attrition from F3 into F2 (thinning and burning) (fig. 1B). Regeneration cuts from types F2 and F3 in year t are denoted d_{12t} and d_{13t} , respectively, creation of new F3 habitat is denoted d_{32t} and re-treatment of F3 habitat is denoted d_{23t} . The thinning-burning decisions are expressed in the transition matrix:

$$\mathbf{V}_t = \begin{bmatrix} 1 & 0 & 0 \\ 0 & 1 - d_{32t} & \tau_{23} - d_{23t} \\ 0 & d_{32t} & 1 - (\tau_{23} - d_{23t}) \end{bmatrix}$$

where columns and rows represent pre- and post-transition states, respectively, and the regeneration decisions are expressed as follows:

$$\mathbf{U}_t = \begin{bmatrix} 1 - \tau_{21} & \max(\tau_{12}, d_{12t}) & \max(\tau_{13}, d_{13t}) \\ \tau_{21} & 1 - \max(\tau_{12}, d_{12t}) & 0 \\ 0 & 0 & 1 - \max(\tau_{13}, d_{13t}) \end{bmatrix}$$

Given the decisions d_{ijt} at time t , the state of the forest \mathbf{f}_t is transformed to a new state \mathbf{f}_{t+1} by first applying the thinning-burning treatments, then the regeneration treatments:

$$\mathbf{f}_{t+1} = \mathbf{U}_t \mathbf{V}_t \mathbf{f}_t$$

We used alternative forms of a simple exponential growth model to express our uncertainty regarding dynamics of the Wood Thrush population occurring in habitats considered favorable (designated F) and unfavorable (\bar{F}). Under one alternative, we assumed that the population of Wood Thrushes in F3 habitat increased (i.e., $F = F3$), whereas that in F2 habitat decreased ($\bar{F} = F2$). We used growth rates for the favorable ($\lambda_F = 1.012$) and unfavorable ($\lambda_{\bar{F}} = 0.949$) habitat quality types consistent with point estimates provided by Powell et al. (2000) for treated and untreated areas, respectively. However, because of high sampling variability, their findings also were consistent with the converse proposition that habitat F2 was favorable and habitat F3 was not. Therefore, the alternative population model used the same parameter values for $\lambda_{\bar{F}}$ and λ_F as

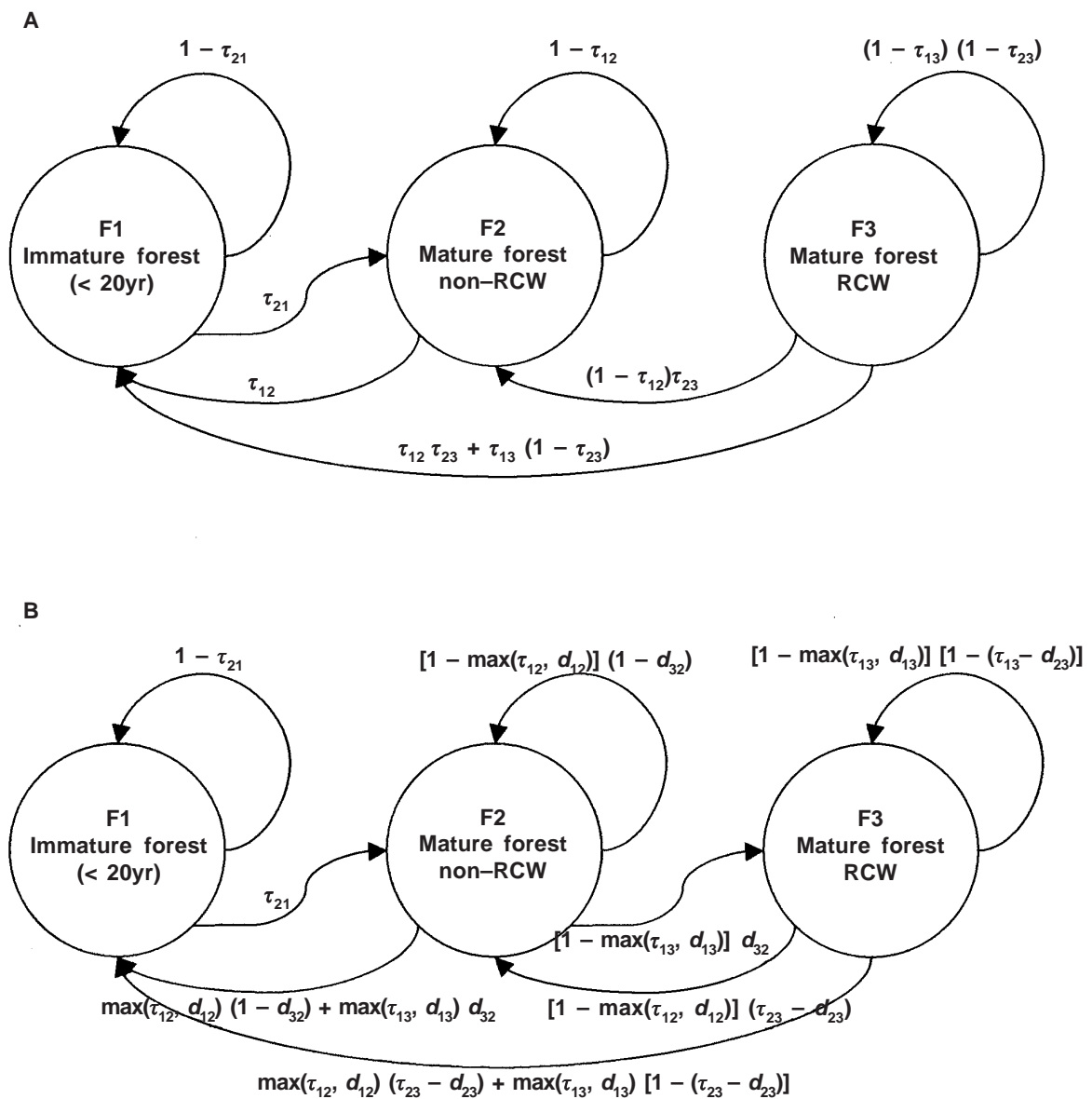


Fig. 1. Model of dynamics among regeneration (F1), mature untreated (F2), and mature forest treated for Red-cockaded Woodpecker use (F3) at PNWR. Portions of the mature forest naturally regenerate every year, and mature classes are augmented by recruitment from the regeneration class. In the absence of management (A), the treated stage F3 reverts back to the F2 stage and ultimately disappears. However, management (B) can reduce this attrition either through treatment of F2 forest or re-treatment of F3 forest. Furthermore, regeneration rate can be increased by cutting from the mature classes.

Fig. 1. Modelo de dinámica entre la regeneración (F1), bosque maduro no tratado (F2), y bosque maduro tratado para su uso en el pájaro carpintero de cresta roja (F3) en PNWR. Algunas áreas del bosque maduro se regeneran anualmente de forma natural, y las clases maduras se aumentan mediante el reclutamiento procedente de la clase de regeneración. En ausencia de gestión (A), la fase tratada F3 revierte a la fase F2 y finalmente desaparece. Sin embargo con gestión (B) se puede reducir este desgaste, bien a través del tratamiento del bosque F2 o del retratamiento del bosque F3. Además, la tasa de regeneración se puede incrementar reduciendo las clases maduras.

before, but switched assignment of F2 and F3 as the unfavorable and favorable habitats. Because Wood Thrushes are not known to commonly use areas of pine regeneration (Roth et al., 1996), we assumed that seral type F1 provided no suitable habitat for Wood Thrushes and therefore ignored this type in the population models. The general expression of the population model was:

$$N_q(t+1) = \lambda_q N_q(t) = \lambda_q \eta_q(t) X_q(t+1), \quad q = F, \bar{F};$$

the latter form expressing population size N at time $t+1$ in terms of bird density η in habitat quality type q at time t and projected proportion X of habitat quality type q at time $t+1$.

Thus, the state of the modeled system is described at any time t by the amount of forest in each seral stage and by the density of Wood Thrushes in types F2 and F3. Given a selection of one of the population models, the steps of the model were as follows: (1) obtain the current forest state (proportional amount of each seral type) and current Wood Thrush densities within types; (2) obtain the current set of forest management decisions given those states; (3) project the state of the forest to the next decision period, given decision set; (4) calculate bird abundances and densities at next decision period, given population model and future forest state; and (5) move to next decision period, repeat 1–5.

Optimization

For both population models, we used dynamic programming to search for a stationary, state-specific optimal decision policy for a suitable conservation-based objective function (Dreyfus & Law, 1977; Williams et al., 2002). We converted expected Wood Thrush abundance at the next time period to a value bounded between 0 and 1:

$$W_t = \max \left(0, \min \left(1, \frac{(N_F(t+1) + N_{\bar{F}}(t+1) - 650)}{(26,000 - 650)} \right) \right)$$

where the constants in the function were based on a minimum acceptable density of 0.05 pairs/ha and a maximum satisfying density of 2.0 pairs/ha over the entire refuge. The objective function was

$$J_t = X_{F3}(t+1)^{0.5} W_t^{0.5}$$

i.e., an equally-weighted geometric average of future proportion of F3 habitat (for woodpecker population viability) and future Wood Thrush abundance value. If decisions drive either component of this objective function to zero, then $J_t = 0$. Because both $X_{F3}(t+1)$ and W_t are bound between 0 and 1, J_t is also bounded between 0 and 1. Dynamic programming seeks those decisions that maximize the sum of this return value over an infinite time frame of decision making ($\sum_{t=0}^{\infty} J_t$). The decision policy found by dynamic programming will be state-dependent,

that is, a set of optimal decisions is associated with each possible system state. A useful decision policy should also be stationary, that is, it should be invariant with regard to which time period a decision is to be made.

We used program ASDP (Lubow, 1995, 1997) to perform the optimization. Because of the unit-sum constraint, compositional state variables such as amounts of forest in three habitat types are not easy to represent in a rectangular matrix of state variable combinations. For example, if X_{F1} and X_{F2} are both allowed to range between 0.0 and 1.0, then the combination $(X_{F1}, X_{F2}) = (0.6, 0.2)$ is a valid system state ($X_{F3} = 0.2$, by subtraction), whereas $(X_{F1}, X_{F2}) = (0.6, 0.5)$ is not. We defined a two-part transformation that expressed the three dependent compositional states in terms of two independent integer states. First, integer indices $l = 1, 2, \dots, 11$ are converted to logits L through a power function:

$$L = p [(l - a) / b]^q$$

where a , b , p , and q are constants chosen to appropriately center, scale, and shape the relationship. Next, the logits are converted to forest type proportions in the usual way:

$$X_i = \exp(L_i) / [1 + \sum \exp(L_j)]$$

Furthermore, because we expected the decision policy to be most sensitive to the Wood Thrush population states when densities were low rather than high, we used square-root transformations of observed densities as state variables.

Program ASDP processes only discrete values of state and decision variables. We discretized both forest composition state variables into 9 levels each and both Wood Thrush state variables into 11 levels each (observed density ranging between 0–2.3 pairs/ha, approximately), yielding 9,801 state combinations. Decisions d_{32} , d_{12} , and d_{13} were each discretized into steps of 0.2 over the range 0.0–1.0, and decision d_{23} was discretized into steps of 0.05 over the range 0.0–0.25. The highly nonlinear structure of the state variables caused overestimates of the objective values under ASDP's linear interpolation and extrapolation features. Though the errors were slight, the compounding of errors over the course of the program's iterations caused difficulty in convergence to stationary policies. Therefore, we imposed a small (0.999) discounting rate on the objective value and terminated the program after 100 iterations, a point at which the number of optimal decisions changing between iterations reached a minimum (16–19 of 9,801 states) and where objective values had not appreciably exceeded their mathematical bounds.

Computation of expected opportunity costs

Our interest was in assessing the outcome of decision making based on observed states of the system

(i.e., observed Wood Thrush densities obtained from unadjusted counts) that may or may not correspond to unobservable true states. We considered four plausible cases of how the relationship between observed densities and true densities of Wood Thrush may vary among habitats: (1) birds are perfectly detectable in F2 and F3 habitats (detection rate = 1.0), (2) birds are equally detectable in F2 and F3 habitats, but not perfectly detectable (detection rate = 0.5), (3) birds are more detectable in F3 habitat (detection rate = 0.7) than in F2 habitat (0.3), and (4) birds are more detectable in F2 habitat (detection rate = 0.7) than in F3 habitat (0.3). Our focus, then, was the assessment of the quality of decision making for cases 2–4 as if case 1 was the operative mode of detection.

For each population model and its associated optimal decision policy, we simulated decision making under each detection model over a 100-year time period. We chose five starting forest states for each simulation: (1) high F1 (initial forest composition $f'_t = [0.60, 0.35, 0.05]$), (2) balanced age class / low F3 ($f'_t = [0.22, 0.73, 0.05]$), (3) balanced age class / high F3 ($f'_t = [0.22, 0.38, 0.40]$), (4) low F1 / low F3 ($f'_t = [0.05, 0.90, 0.05]$), and (5) low F1 / high F3 ($f'_t = [0.05, 0.55, 0.40]$). For starting Wood Thrush density states, we chose 0.5 pairs/ha for both F2 and F3 habitats. Because the decision models were all deterministic, multiple simulation runs were not required.

Cumulative 100-year values of J were obtained for each detection scenario, annualized (divided by 100), and compared to the annualized cumulative J value for the model of perfect detection. Thus, three comparisons were available for each population model and starting state. If $j_A - j_B$ represents the difference in annualized J values for two scenarios A and B, then the maximum difference attributable to either the $X_{F3}(t+1)$ or the W components of the objective function (when the other component is held fixed) is $1 - (j_B / j_A)^2$. Expressed as a percentage, this value can be interpreted as the maximum percent loss, or partial opportunity cost, incurred by one of the resources under suboptimal management. For example, a partial opportunity cost of 10% implies that either woodpecker habitat amount or Wood Thrush abundance is reduced by as much as 10% if decision making is made under an inappropriate detectability assumption. Also, we averaged the $j_A - j_B$ differences over the alternative detection scenarios to represent expected resource cost under complete uncertainty with respect to the detection models. This statistic closely resembles the value of information (Lindley, 1985), an estimate of expected loss when one lacks the information to distinguish among alternative expected outcomes of decision making (here, alternative detection scenarios). For example, an expected partial opportunity cost of 10% implies that the sacrifice in either woodpecker habitat or Wood Thrush abundance is expected to average 10% over several plausible but uncertain detection relationships.

Results

In the population model that considered F3 as favorable habitat for Wood Thrushes, optimal annualized cumulative returns for the model of perfect detection ranged 0.412–0.466 over the five starting states (table 1). Corresponding values for the models of equal detection and higher detection in F3 were comparable, even greater in some cases (table 1). This outcome suggests that our decision policy was suboptimal, likely a consequence of difficulties in the optimization routine described earlier. However, the returns under the alternative detection models are in close agreement, suggesting that, at least for these two models of imperfect detection, management based on uncorrected counts or densities was as profitable as management under perfect detection.

However, the model of lower detection in F3 generated lower annualized returns than did the model of perfect detection (table 1; detection model M3). Differences in returns appear small (0.007–0.014), but they translate into partial opportunity costs of 3–6% for either of the resource components (table 1). Averaging the differences over the three models of imperfect detection suggests expected partial opportunity costs of 1–3% under model uncertainty (table 1).

For the model proposing F2 as favorable habitat, annualized returns for the model of perfect detectability ranged 0.236–0.268 (table 1). Simulation of each of the models of imperfect detection provided lower annualized returns in all cases (table 1). The smallest differences in returns occurred for the model of lower detection in F2 (0.0–0.003), intermediate differences were observed for the model of equal detectability between habitats (0.002–0.008), and the greatest differences occurred for the model of lower detection in F3 (0.003–0.015) (table 1). The largest value of partial opportunity cost was 11% (table 1). Averaging over all the models of imperfect detection yielded 2–6% in expected partial opportunity cost (table 1).

Discussion

Whether unadjusted counts constitute reliable indicators of wildlife population abundance has been an issue of recent intensive debate (Thompson et al., 1998; Hutto & Young, 2002; Engeman, 2003; Anderson, 2003). Perhaps one reason that the arguments persist is that the extra costs associated with collecting the ancillary data to estimate detection rate are tangible and easy to perceive, whereas consequences of decision making based on faulty detectability assumptions are not. This "invisible cost" of misled management may be inappropriately taken by some as evidence that such costs are negligible and perhaps contributes to a complacency toward the problem of unmeasured detection biases. Our analysis of a very simple population model under quite reasonable alternative patterns

Table 1. Annualized cumulative objective values for a combined model of forest management and Wood Thrush response, under each of four alternative forms of Wood Thrush detection rate, two alternative Wood Thrush population models, and for five initial forest states. One population model projected positive population growth in forest type F3 and negative growth in type F2, and the other model projected the converse. Detection models were: M0. Perfect detectability; M1. Detection rate of 0.5 in F2 and F3 habitats; M2. Detection rate of 0.3 in F2 habitat and 0.7 in F3 habitat; M3. Detection rate of 0.7 in F2 and 0.3 in F3; Av. Averaged. Partial cost is the maximum difference in objective function value for either of the contributing components of the objective function (amount of F3 habitat, Wood Thrush abundance value), holding the other component fixed.

Tabla 1. Valores anualizados de los objetivos acumulativos para un modelo combinado de gestión forestal y respuesta de los zorzales mustelinos, según cada una de las cuatro formas alternativas de su tasa de detección según dos modelos alternativos de población y según cinco estados forestales iniciales. Un modelo poblacional proyectó un crecimiento de población positivo en el bosque del tipo F3 y un crecimiento negativo en el del tipo F2, mientras que el otro modelo proyectó lo opuesto. Los modelos de detección fueron: M0. Detectabilidad perfecta; M1. Tasa de detección de 0,5 en los hábitats F2 y F3; M2. Tasa de detección de 0,3 en el hábitat F2 y de 0,7 en el hábitat F3; M3. Tasa de detección de 0,7 en F2 y de 0,3 en F3 (M3); Av. Promedio. El coste parcial es la diferencia máxima en el valor de la función de objetivos para cada uno de los componentes que contribuyen a dicha función (total de hábitat F3, valor de abundancia de los zorzales mustelinos), manteniendo fijo el otro componente.

Population model Initial forest state	Cumulative value (annualized)				Partial cost			
	M0	M1	M2	M3	M1	M2	M3	Av
$\lambda_{F3} > 1, \lambda_{F2} < 1$								
High F1	0.412	0.407	0.409	0.404	0.024	0.014	0.042	0.027
Balanced age, low F3	0.442	0.440	0.443	0.429	0.007	-0.007	0.058	0.020
Balanced age, high F3	0.441	0.440	0.443	0.427	0.007	-0.007	0.063	0.021
Low F1, low F3	0.459	0.462	0.459	0.452	-0.012	-0.001	0.031	0.006
Low F1, high F3	0.466	0.467	0.466	0.459	-0.005	-0.002	0.028	0.007
$\lambda_{F3} < 1, \lambda_{F2} > 1$								
High F1	0.236	0.234	0.234	0.233	0.016	0.021	0.028	0.021
Balanced age, low F3	0.256	0.254	0.256	0.249	0.018	0.002	0.053	0.025
Balanced age, high F3	0.255	0.254	0.255	0.248	0.014	0.000	0.057	0.024
Low F1, low F3	0.268	0.259	0.265	0.253	0.061	0.019	0.108	0.063
Low F1, high F3	0.268	0.264	0.265	0.257	0.025	0.019	0.075	0.040

of detection bias demonstrates that uncertainty with respect to detectability results in some degree of opportunity cost that is measurable in units of the resource.

The opportunity costs we observed were small (all partial costs < 11%), but two points are worth noting. First, opportunity costs will certainly vary according to choice of population model, detection model, and objective function. For example, partial costs become as large as 24% if we reduce detection rate from 0.3 to 0.1 in one of the detection models and increase its counterpart rate from 0.7 to 0.9. Second, a given cost may have different implications in different management settings. For example, an 11% cost in habitat or population value may be inconsequential in many management settings, but not in all, particularly in endangered species management. If F2 habi-

tat is favorable for Wood Thrushes and yields greater detectability than does F3 habitat, our model suggests that up to 11% of Red-cockaded Woodpecker habitat (type F3) could be needlessly sacrificed if management decisions are inappropriately based on the assumption that Wood Thrushes are equally detectable in both habitats. In this case, the erroneous implication of observing equal densities of Wood Thrushes in F2 and F3 habitats is that the total population density is too far below the satisfying density and should be increased by removing some of the unfavorable (F3) habitat and creating more of the favorable (F2) habitat.

Our analysis dealt only with detection bias in the form of undercounting, whereas many monitoring programs may collect information also prone to overcount bias. For example, in many programs,

an individual or its sign (tracks, fecal pellets, etc.) may be counted more than once, and these counts are often considered to represent a consistent overrepresentation of a smaller number of individual animals (Diefenbach et al., 1994). We know of no reason to expect that such biases would result in opportunity costs of similar magnitude to our findings; indeed, it is the opinion of one reviewer that undercounting, constant or otherwise, may be the least problematic form of count bias. Confirmation of such speculation must wait until these detection scenarios are explicitly modeled.

When a monitoring program of uncorrected counts is considered for the support of management decision making, we recommend the construction and exploration of decision models such as these to fully estimate the true costs of conducting that form of monitoring. Our suspicion is that opportunity costs of biased monitoring often will not be negligible, even under mild departures from the assumed proportionality relationship. We also suggest that costs of estimating detection rate will often be less than the total of the collection cost of uncorrected counts plus the opportunity cost of decision making based on those counts. Even where the cost of uncorrected counts is anticipated to be low relative to the cost of correcting them, the relationship between the count and true density should at least occasionally be monitored.

Previous authors have suggested approaches to determining if or how much detection probability varies across time or space (see Skalski & Robson, 1992; MacKenzie & Kendall, 2002). However, this paper is a first attempt at directly evaluating the implication of this variation in terms of management objectives

More generally, this study was a first step in exploring the proper consideration of monitoring effort and design in making decisions. We have focused on the effect of bias in indices of system state on an optimal policy and its consequences for the system. We have not considered the relative precision of adjusted and unadjusted counts, and its impact on system response in terms of objectives. Wildlife systems are managed in the face of four sources of uncertainty (Nichols et al., 1995): environmental variation, partial controllability (a given decision has variable impact on the system), structural uncertainty about the key factors that drive the system, and partial observability (sampling variability and estimation bias).

Reduction of partial observability should improve decisions directly by giving the manager a clearer picture of system status. This reduction also provides the indirect benefit of helping to reduce structural uncertainty. The cost/benefit of different approaches to monitoring (both in terms of sampling effort which controls precision and the types of data collected to reduce bias) could be incorporated directly into the decision model by making these alternative monitoring decisions part of the general decision space, and incorporating the cost of monitoring into the objective function.

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