EcoHealth
DOI: 10.1007/s10393-015-1094-4

EcoHealth

Original Contribution

Monitoring for the Management of Disease Risk in Animal Translocation Programmes

James D. Nichols,[1] Tuula E. Hollmen,[2,3] and James B. Grand[4]

[1]*Patuxent Wildlife Research Center, U.S. Geological Survey, Laurel, MD 20708*
[2]*Alaska Sea Life Center, Seward, AK*
[3]*University of Alaska, Fairbanks, AK*
[4]*Cooperative Fish and Wildlife Research Unit, U.S. Geological Survey, Auburn, AL*

Abstract: Monitoring is best viewed as a component of some larger programme focused on science or conservation. The value of monitoring is determined by the extent to which it informs the parent process. Animal translocation programmes are typically designed to augment or establish viable animal populations without changing the local community in any detrimental way. Such programmes seek to minimize disease risk to local wild animals, to translocated animals, and in some cases to humans. Disease monitoring can inform translocation decisions by (1) providing information for state-dependent decisions, (2) assessing progress towards programme objectives, and (3) permitting learning in order to make better decisions in the future. Here we discuss specific decisions that can be informed by both pre-release and post-release disease monitoring programmes. We specify state variables and vital rates needed to inform these decisions. We then discuss monitoring data and analytic methods that can be used to estimate these state variables and vital rates. Our discussion is necessarily general, but hopefully provides a basis for tailoring disease monitoring approaches to specific translocation programmes.

Keywords: capture–recapture modelling, conservation decisions, disease risk, monitoring programme, occupancy modelling, translocation programmes

Introduction

The monitoring of animal populations and communities has become a common activity, with many different kinds of programmes implemented for a variety of reasons. Some monitoring programmes are very useful, whereas many are not. Our perspective is that monitoring should not be viewed as a stand-alone activity, but rather as a component of a larger process, typically focused on either science or management. The key to successful monitoring is to then tailor the monitoring programme to the needs of this larger process. This tailoring first requires an answer to the question "why monitor", followed by a focus on the questions "what to monitor" and "how" (Yoccoz et al. 2001). Animal reintroduction and augmentation programmes are increasingly used to support wildlife conservation goals. Risk of disease transmission is considered a key factor in planning many such conservation translocation programmes. Here we focus on monitoring designed to inform efforts to manage disease risk in conservation

Correspondence to: James D. Nichols, e-mail: jnichols@usgs.gov

Published online: 14 January 2016

translocation programmes. We will structure the paper sequentially around responses to the above three questions, ''why'', ''what'', and ''how''.

Monitoring for Conservation: A Conceptual Framework

Animal translocation is an action that is virtually always associated with some sort of conservation issue. Conservation programmes are themselves examples of decision processes, and a brief overview of the decision framework should be useful for understanding the role of monitoring in such a process. Decision processes require at least the following components: objectives, potential actions, models, monitoring, and a decision algorithm. *Objectives* should provide a clear statement of what is to be achieved by the process. Some practitioners distinguish between ''fundamental'' objectives, which constitute the ultimate or endpoint goals of the programme, and ''means'' objectives, which are intermediate goals required to achieve the fundamental objectives. The ultimate objective of many conservation programmes is a healthy, sustainable system that includes populations of certain species. We prefer not to use the terminology of the fundamental versus means dichotomy, but will instead focus on specific objectives that contribute to this ultimate objective.

Potential actions refer to the things that can be done in order to meet or move towards objectives. The decision problem is typically to decide what action to take at a given point in time. *Models* refer to means for predicting the consequences of potential actions to the managed system. Models are frequently mathematical, facilitating analysis, but they include all possible means of making predictions (e.g. they may reside only in the brain of the manager). *Monitoring* provides estimates of key variables and vital rates of the system, and the roles played by such estimates are described more fully below. Finally, the *decision algorithm* is a means of using the other system components to derive a good or even optimal decision.

Animal translocation programmes typically entail decisions that are recurrent and characterized by uncertainty. *Recurrent* decisions are those made not just once, but at multiple times (decision points). Most programmes of animal translocation will involve not just a single release of animals to an area, but releases on multiple occasions (e.g. every year). *Uncertainty* frequently characterizes the modelling of how translocated animals affect dynamics of the system to which the animals are introduced. For example, if hard and soft release methods are being considered, we would like our models to project the survival rate and eventual probability of being recruited into the target population for the different release methods being considered. Recurrent decisions offer the possibility of learning, that is of discriminating among competing models of system response to different translocation methods, for example.

In the absence of other information, a request to ''design a monitoring programme'' for a particular system admits an extremely large number of possibilities, with no means of deciding among them. In contrast, design of a monitoring programme to serve as a component of a larger decision process is much more focused and is essentially inherited from the specifics of the larger process. The monitoring programme is designed for the specific purpose of providing estimates that play well-defined roles in the decision process (see below).

Why Monitor

General Framework

Decision processes for ecological management or conservation typically focus on state variables that characterize the current status of the managed system relative to programme objectives. Examples of state variables include such entities as population size, species richness, proportion of a population infected with a disease organism, etc. Monitoring designed to inform decision processes is then often focused on estimating the state variables themselves, the vital rates responsible for state variable dynamics, and the effects of management actions on these vital rates. Such monitoring typically serves three distinct roles in programmes of management or conservation (e.g. Yoccoz et al. 2001; Nichols and Williams 2006). The first is provision of estimates of state variables for the purpose of making state-dependent decisions, that is, decisions that depend on estimates of system state variable(s). For example, once population size has reached a certain level such that we can view the population as ''established'', we would likely consider ceasing efforts to increment the population with translocated animals. The second is provision of estimates of state variables and other variables relevant to objectives in order to assess progress and success of the management process. The third is provision of estimates of state vari-

ables and vital rates for the purpose of learning. The third role of monitoring (learning) is based on a scientific approach to reducing uncertainty. Management and conservation of natural resources are frequently characterized by substantial uncertainty, resulting in the use of multiple competing models in the management process (e.g. Johnson et al. 1993; Nichols 2001). Such multiple models represent competing hypotheses about how management actions translate into system dynamics, with the relative influence of different models defined by accumulated evidence as reflected by so-called "model weights". These weights are simply numbers between 0 and 1, summing to 1 for all the members of the model set, each reflecting the relative weight of evidence that has accumulated for the respective model. Evidentiary changes in model weights are based on the differences between model-based predictions, made at each decision point at which an action is taken, and the estimates of state variables and vital rates obtained via monitoring following the action. This approach to learning follows the traditional approach to science (Platt 1964), essentially embedding a scientific step in the larger decision process. Accumulation of evidence is based on Bayesian updating of these model weights using the prior (to the monitoring) weight and the new evidence based on the comparison of predictions and monitoring estimates (Johnson et al. 1993; Nichols 2001). Model weights directly determine the relative influence of each model in the decision process, and this real-time updating insures that the learning that occurs following each bout of monitoring is immediately used in the subsequent decision (e.g. see Johnson 2011). In addition to this focal role in learning, monitoring provides estimates of vital rates and of parameters describing relationships between vital rates and management actions. Such estimates are used to develop and periodically update system models, uses that can also be viewed as learning.

The above three stated uses of monitoring were written very generally, and specifics for any management or conservation programme are derived from the specific objectives of that programme. Animal translocation programmes can include a number of specific objectives, but two that are common to most such programmes are as follows: (1) augmentation of existing populations or establishment of new populations and (2) minimization of the spread of disease from released animals to wild conspecifics or members of other species. Monitoring designed to inform the first objective of augmentation or establishment has been discussed elsewhere (Nichols and Armstrong 2012). The remainder of this paper will be focused on the objective of minimizing disease risk, with a primary focus on minimizing the risk of exposing wild animals to pathogens carried by translocated animals (objective 2). However, we also consider monitoring for minimizing disease exposure risk from wild animals to translocated animals, contributing to objective (1) of augmenting or establishing populations in the wild.

Pre-release Disease Monitoring

Pre-release monitoring of animals to be translocated will be common to most translocation programmes for which disease is viewed as a potential problem. Disease assays can be used to draw inferences about disease state of each individual to be released, where "disease state" (v_i^x for individual i, pathogen x) might simply refer to the states used in classical epidemiological modelling (e.g. Kermack and McKendrick 1927). When only a single disease or parasite is of concern, a diagnostic assay would be used to categorize a potential release animal as susceptible (state S), infected (I), or recovered/resistant (R) for each animal to be released. If inferences are drawn about multiple pathogens, then the multivariate state could be depicted as $\mathbf{v}_i = (v_i^1, v_i^2, \ldots, v_i^L)$ for L pathogens. For simplicity of discussion, we will drop the pathogen-specific superscripts and focus on a single, generic pathogen, but the framework is much more general than this.

Information on disease state of individuals intended for release is used for both state-dependent decisions and learning. A primary decision is simply whether to release the individual or not. In the case of high-risk pathogens, individuals in the infected state would likely be withheld and not released into the wild. In the case of some pathogens, another decision might be to treat the animal in some manner and then release it. Disease states of animals intended for release can be used to learn about the effectiveness of various pre-release treatments such as immune boosters and antibiotics. Models of the effectiveness of such treatments would lead to predictions about expected numbers of post-treatment, infected individuals. Comparison of inferred disease states with these predictions can be used to learn which models predict well and which treatments are most effective.

In many cases, monitoring of disease state of wild individuals during the pre-release period may be useful in informing release decisions. For example, pre-existence of a specific pathogen in the wild population (conspecifics or related species) may reduce the concern of releasing indi-

viduals with this pathogen. If a pathogen found in animals intended for release is alien to the wild population, then a decision not to release infected birds may be more likely. Pre-release monitoring of wild individuals and their disease states, combined with post-release monitoring, will also be useful in assessing the degree to which releases may have changed survival rates and the distribution of disease states within the wild population, another example of the learning role of monitoring.

Post-release Disease Monitoring

Monitoring of both translocated and wild individuals and their disease states post-release should be useful in informing decisions, assessing programme performance, and learning. Monitoring of translocated individuals can be used to draw inferences about disease states, state transition probabilities, and state-specific survival rates. Such inferences will be especially useful for learning. For example, in addition to the risk of introducing novel pathogens to wild populations, pre-existing pathogens in wild populations may pose a threat to translocated animals that have been reared in a more sterile and managed captive environment. Competing models of the magnitude of such effects can be informed by estimates of state transition probabilities (e.g. from susceptible to infected and from infected to recovered/resistant), and state-specific survival rates of translocated individuals. Similarly, such monitoring can inform models of the effectiveness of such pre-release treatments as providing exposure of captive animals to such pathogens or immunizing animals to enhance their survival and success. The utility of these various kinds of learning depends on the recurrent nature of conservation translocation programmes, such that learning at one time can be used to make better decisions for future releases.

Post-release disease monitoring of wild animals in the vicinity of the release site would likely be focused as well on inferences about disease states, state transition probabilities, and state-specific survival rates. The distribution of disease states in potentially affected wild populations at various times post-release can inform state-dependent decisions about whether to continue releases, with large increases in infected animals, and associated transitions to infected, perhaps warranting more careful treatments of birds pre-release, disease response and control in the wild, or even cessation of translocations. Such monitoring of wild birds would also permit learning about competing models of disease transmission and effects used in the decision process. Learning could also include the effectiveness of pre-release treatments in achieving the ultimate objective of minimal effects on wild populations.

In some situations, post-release disease monitoring of wild animals may also be useful in neighbouring areas extending beyond the release location. Such monitoring would focus on estimating disease state for samples of animals from these neighbouring locations, but might not require the detailed repeat sampling of individuals needed to draw detailed inferences about state transition probabilities and state-specific survival (see subsequent discussion of ''how'' to monitor). This information could be used for state-dependent decisions. For example, rapid spread of pathogens across space could result in decisions to either provide increasingly rigorous pre-release treatments or else stop releases altogether. Such monitoring would facilitate learning about competing epidemiological models of disease spread and dynamics, perhaps as influenced by different pre-release treatments.

Disease Monitoring for Conservation Translocation Programmes: Why?

So, the primary roles of disease monitoring within conservation translocation programmes are to make state-dependent decisions and to learn about relevant processes, especially treatment effectiveness and disease dynamics and effects. In addition, monitoring can provide information about how well the objective of minimizing the spread of pathogens to wild animals is being accomplished, and can provide parameter estimates for populating models of disease dynamics. We have subdivided monitoring efforts according to temporal sequence (before or after releases) and focal animals (translocated animals and wild animals) and have described some key state-dependent decisions informed by these classes of monitoring. In addition, we have noted the utility of such monitoring for learning, that is discriminating among competing hypotheses about topics ranging from pre-release treatment effectiveness to disease dynamics and effects. Our discussion has been very general, with all described monitoring likely not needed for all translocation programmes. Rather, the recommendation is for the designers of any specific conservation translocation programme to consider monitoring needs from this perspective of exactly how resulting data are to be used in the decision process. Armed with a clear idea of the explicit role of monitoring in the process, decisions about what and how to monitor become much easier.

What to Monitor

The answer to the question "what should be monitored" is inherited directly from the answer to the question, "why monitor". For disease monitoring designed to inform decisions about animal translocation programmes, the relevant state variables will usually be the number or proportion of individuals in each of the relevant disease states, for example, susceptible, infected, and recovered/resistant. These state variables will frequently be of interest for both translocated and wild animals. Changes in these state variables are determined by state-specific vital rates that will be another target of monitoring for conservation translocation programmes. These vital rates include state-specific survival rates and probabilities of transitioning from one disease state to another.

How to Monitor

General Framework

Monitoring of animal populations typically entails counts of some sort. Translation of these count data into inferences about state variables and vital rates usually entails dealing with two primary sources of variation: spatial variation and detection probability (e.g. Williams et al. 2002). Spatial variation refers to variation in animal state variables (e.g. population size and numbers of animals in different disease states) over space and is especially important when the entire area about which inferences are to be drawn cannot be surveyed. In such cases, space must be sampled in such a manner that inferences can be drawn about locations that are not surveyed based on count data from locations that are surveyed. This kind of inference usually requires that the investigator select spatial units to be sampled probabilistically, such that an *a priori* probability of selection is available for each spatial unit in the area of interest. Simple random sampling and stratified random sampling are two commonly used spatial sampling designs, but a variety of probabilistic sampling approaches has been developed (e.g. Thompson 2002). Much initial monitoring associated with conservation translocation programmes will be conducted in the proximity of the release site, such that the issue of spatial sampling will not be so important, at least very early in the programme. However, movement of translocated animals and associated pathogens from the release site should be considered in the development of a monitoring programme in longer term. For migratory species, monitoring may include specific locations distant from the release site.

The second source of variation in counts, detection probability, is pervasive in the study of animal populations and communities. It refers to the reality that virtually any count of animals in any location is likely to be incomplete; that is, some animals will be missed and go undetected. In some kinds of studies, including much disease monitoring, we generalize the concept of detection probability to include the possibility of misclassification (i.e. assigning an animal to one disease state when it is actually in another). Inference about state variables and vital rates then requires the ability to somehow incorporate detection probability into models used to develop estimators of these focal quantities. Stated differently, count data are recognized to result from two kinds of processes, the ecological process of interest, and the survey process used to obtain data (Royle and Dorazio 2008). Models on which inferences are to be based must include both kinds of process. This issue of detection probability must be dealt with in monitoring focused on the objective of population augmentation or establishment (Nichols and Armstrong 2012) as well as the objective of minimizing disease risk.

Our description of methods that we believe to be potentially useful for the monitoring of disease risk and dynamics will focus on ways of dealing with variation in detection probability. Not only do we expect to be unable to count all animals in any disease state, for example, but we also expect variation in detection probability associated with disease state itself. The methods described below deal with this source of variation in a manner that should permit estimation of the quantities of interest.

Disease Dynamics Within Populations

The state variables of interest in disease monitoring will be the numbers of animals in each of three disease states, N^v where $v = S$ (susceptible state), I (infected), and R (recovered/resistant). These state variables are relevant to both translocated animals and wild animals, but we include no extra notation for this distinction, as the inference methods are the same for both groups of animals. In some cases, it is the proportions of individuals in each disease state that are viewed as state variables. The term *prevalence* is frequently used to refer to the proportion of animals in a population that is in the infected state.

The vital rates of primary interest are the state-specific survival rates, S_t^v = Pr(animal alive and in local population

at time t+1 | animal in disease state v and present in population at time t), and state transition probabilities, ψ_t^{vw}= Pr(animal in state w at time t+1 | animal in state v at time t and still alive and in local population at t+1). The actual transition probabilities of interest in a particular translocation programme will depend on the focal pathogen and its dynamics. For example, SIR models (Kermack and McKendrick 1927) for many pathogens would include the following constraints: $\psi_t^{SR} = \psi_t^{IS} = \psi_t^{RS} = \psi_t^{RI} = 0$. For such pathogens, primary interest would be on the nonzero probabilities, ψ_t^{SI}, ψ_t^{IR}. For example, ψ_t^{SI} is an important determinant of disease dynamics, governing the rate of transmission and spread. It will be especially useful to develop models of vital rates (e.g. ψ_t^{SI} and S_t^I) as functions of management actions (immunization) and key environmental covariates (e.g. seasonality and weather, environmental reservoirs).

The monitoring methodology for developing inferences about these state variables and vital rates will entail capturing animals, marking them individually, and then either recapturing or resighting them in subsequent sampling occasions. Disease state must be ascertained at each detection, ruling out use of resightings with these models for pathogens that can only be detected using methods (e.g. blood samples) that require handling animals. For some pathogens (e.g. conjunctivitis [*Mycoplasma gallisepticum*] of house finches [*Haemorhous mexicanus*], Faustino et al. 2004), disease state can be assessed simply by direct observation without actually capturing the animal. Data resulting from this sort of monitoring programme are typically summarized as detection histories for each individual that is captured, marked, and released. These detection histories contain information on the sampling occasions at which the individual is detected and the disease state at that time. For example, a detection history of h_i = (0 S 0 S I 0) would indicate an animal (individual i) that was captured, determined to be in the susceptible state, and released at occasion 2 of a 6-occasion programme. The individual was not detected at sampling occasions 1, 3, or 6. It was detected at occasions 4 and 5, and determined to be in the susceptible state at occasion 4 and the infected state at occasion 5.

The natural inference framework for monitoring data (e.g. detection histories) of this sort is provided by multistate capture–recapture models (e.g. Arnason 1972, 1973; Brownie et al. 1993; Schwarz et al. 1993; Lebreton et al. 2009). Cooch et al. (2012) review use of this approach to study SIR disease dynamics, and applications to animal populations include Faustino et al. (2004), Senar and Conroy (2004), Lachish et al. (2011), Murray et al. (2009), and Ozgul et al. (2009). The parameters of this class of models that are relevant to disease processes are the state-specific survival rates and the transition probabilities described above. The other parameters of these models are the state-specific detection probabilities, reflecting the probability that an animal in disease state v at time t is detected, p_t^v. These state-specific survival, transition, and detection parameters are used to develop a model for the probability of any possible detection history, conditional on initial release of an animal in whatever state, v. The likelihood is formed as the product of these history-specific probabilities over all animals that are initially captured and released and provides the basis for inference about model parameters. Estimation can be accomplished using programmes such as MARK (White and Burnham 1999), ESURGE (Choquet et al. 2009), and WinBUGS (Kery and Schaub 2012).

The vital rates relevant to *SIR* disease dynamics, state-specific survival, and transition probabilities, can be directly estimated via maximum likelihood (e.g. see Lebreton et al. 2009). The state variables, e.g. numbers or proportions of individuals in each disease state, are estimated as follows. Define n_t^v as the number of animals detected at time t and determined to be in disease state v, and N_t^v as the quantity of interest, the number of animals in the population at time t in disease state v. Estimates of state-specific detection probabilities are used to translate the numbers detected into estimates of state-specific abundance as:

$$\hat{N}_t^v = n_t^v / \hat{p}_t^v, \tag{1}$$

where the hats denote estimators. Equation (1) is simply the canonical estimator for animal abundance of animal population ecology (Lancia et al. 1994; Williams et al. 2002). If we prefer to view proportions of individuals in each state as the focal state variable, then these can be estimated as follows:

$$\hat{\delta}_t^v = \frac{\hat{N}_t^v}{\sum_v \hat{N}_t^v}. \tag{2}$$

Disease prevalence would thus be estimated using (2) for $v = I$ (also see Cooch et al. 2012). If p_t^v are similar for all disease states, v, then Eq. (1) is not needed to estimate state-specific proportions, which can be estimated directly from the detection statistics, n_t^v. However, in most cases, where investigators have actually estimated state-specific detection probabilities, they have varied among different disease states (Faustino et al. 2004; Senar and Conroy 2004;

Jennelle et al. 2007; Conn and Cooch 2009; Murray et al. 2009; Ozgul et al. 2009).

Multistate capture–recapture models described above make assumptions that are potentially restrictive for some investigations of disease dynamics. For example, the classical models assume that state is unambiguously assigned to each detected individual. However, it will not be unusual for disease monitoring programmes to include two detection methods, one of which permits unambiguous assignment of disease state (e.g. capture and disease assays based on blood samples) and the other of which does not (e.g. direct observation without capture, permitting an imperfect state assignment that is subject to error). Such programmes would require use of state uncertainty models, with state assignment certain for one method and uncertain for the other. Another possibility entails the use of a single detection method that is subject to error, but the error rate is "known" or estimated using data from some source other than the monitoring programme. Models for these situations were initially developed by Kendall et al. (2003, 2004) and later generalized by Pradel (2005). Estimation can be based directly on likelihoods that can be viewed as special cases of hidden Markov models and state space models. Key features of such models are sampling parameters that include not only nondetection ($1 - \hat{p}_t^v$), but also misclassification (the probability that an animal classified as belonging to state v is actually in state w; this concept includes so-called "false positives"), and mixture probabilities that reflect the true proportions of newly marked individuals at each sampling occasion that occurs in each disease state. Programme ESURGE (Choquet et al. 2009) can be used to provide estimates for state uncertainty models based on detection histories consisting of observed (sometimes with error) state assignments. Conn and Cooch (2009; also see Cooch et al. 2012) provide a nice example of such a model admitting disease state uncertainty in some observations.

An additional assumption of general multistate models is that all states are potentially observable, i.e. that $\hat{p}_t^v > 0$ for all v. It is possible that some pathogens may render infected animals completely unobservable (e.g. immobile in hiding places such as burrows). In such situations, transitions to and from the unobservable state can be estimated using data collected under Pollock's (1982) robust design, in which secondary sampling occasions occur within each primary sampling occasion (Kendall et al. 1997). Even with standard open-model data (a single sampling occasion at each primary period), it is sometimes possible to estimate transitions to and from an unobservable state using models with some parameters constrained to be constant over time and/or state (Kendall and Nichols 2002). Both classes of model (for robust design data; for standard open-model data) can be implemented using programme MARK (White and Burnham 1999).

Disease Dynamics Across Space

In the event that pathogens from released individuals do become established in local population(s) of wild animals, monitoring the spatial extent and spread of the pathogens can inform both state-dependent decisions and learning. Monitoring designed for this purpose will focus on spatial units defined either naturally (e.g. patches of suitable habitat) or by superimposing a uniform grid on the focal landscape. The state variables of interest will be the proportion (or number) of spatial units at sampling occasion t containing potentially affected host species but no pathogens (θ_t^H), containing both host species and the pathogen (θ_t^D), and containing neither pathogens nor the host species ($\theta_t^0 = 1 - \theta_t^H - \theta_t^D$). If it is possible for the pathogen to persist in the environment in the absence of the host species, then we would add another state for spatial units that contain only the pathogen.

The vital rates underlying disease dynamics across space are transition probabilities governing changes in the disease state associated with a spatial unit. For example, transition probability φ_t^{HD} = Pr (spatial unit is in state D at time $t+1$ | unit was in state H at time t) will be especially relevant to the effects of translocation disease risks on the system in which releases are occurring. Disease risk management in translocation programmes will try to minimize φ_t^{HD} for the local spatial unit receiving the releases, as well as for neighbouring units. Consequences of the pathogen for host occupancy dynamics can be assessed, for example, via a comparison of estimates of φ_t^{D0} and φ_t^{H0}, reflecting local extinction of the host species when the pathogen is present and absent.

Field sampling in each spatial unit will entail detecting, and usually capturing, individuals of potential host species and conducting diagnostic tests directed at detecting the pathogen(s) of interest. Detection history data are recorded as either no detections of the potential host species (observation state = 0), or at least one individual of a potential host species detected, with no pathogen detections via

diagnostic tests (observation state H) or at least one pathogen detection (D). Such data are summarized for each spatial unit, i, as a detection history, similar to those used for capture–recapture data. For example, $h_i = (0\ H\ H\ 0\ D)$ denotes a unit sampled at five different occasions, with no detections of hosts on occasions 1 and 4, detection of host but no pathogen on occasions 2 and 3, and detection of hosts with pathogen on occasion 5.

Inferences about these spatial state variables and vital rates can be made using multistate occupancy models (Royle 2004; Royle and Link 2005; MacKenzie et al. 2006, 2009; Nichols et al. 2007). Model parameters associated with disease dynamics include the state variables of interest, θ_t^v, and associated state transition probabilities, φ_t^{vw}. In addition, these models require detection/classification probabilities associated the different states, p_t^{vw}, where v denotes the observed state of the unit and w denotes the true state. Thus, p_t^{HD} indicates the probability of observing the host species at sampling occasion t, but not the pathogen, for a unit in which the pathogen was present, p_t^{HD} = Pr(host detected, but not the pathogen | both host and pathogen present). These process and sampling parameters are used to develop probabilities associated with each observed detection history, and the product of these probabilities represents the likelihood from which inference is made. Implementation of these models is possible using programmes PRESENCE (Hines 2006), MARK (White and Burnham 1999), and WinBugs (Kery and Schaub 2012).

The recommendation (MacKenzie et al. 2006; McClintock et al. 2010) to use occupancy modelling for investigations of spatial epidemiology has led to a number of recent applications (Adams et al. 2010; Gomez-Diaz et al. 2010; Lachish et al. 2011; Miller et al. 2012; Bailey et al. 2014; Elmore et al. 2014). An extension of occupancy modelling that is likely to be useful for drawing inferences about possible spatial spread of pathogens based on translocation programme monitoring is so-called ‘‘autologistic modeling’’ (e.g. Royle and Dorazio 2008; Bled et al. 2011, 2013; Yackulic et al. 2012). If pathogens are introduced through releases of animals into a spatial unit, then pathogen spread will often be expected to radiate outward from this unit to local neighbouring spatial units (Skellam 1951). Autologistic modelling entails the modelling of transition probabilities for a spatial unit as a function of the number of neighbouring units that are occupied by the focal entity (pathogen in this case). Thus, φ_t^{HD} and φ_t^{0D} could be modelled as a function of average θ_t^D for neighbour spatial units. Neighbourhood can be defined in any number of ways (e.g. Eaton et al. 2014), including the possibility of considering all spatial units in the overall area of interest weighted by the inverse of their respective distances from the focal unit. In the case of disease dynamics, the definition of neighbourhood will likely depend on transmission dynamics of specific pathogens of concern. This neighbourhood approach to autologistic modelling can be implemented using programme PRESENCE (Hines 2006). We believe that this type of modelling may prove especially useful for learning about the spatial spread of pathogens that are inadvertently introduced, a key issue in the consideration of disease risk associated with conservation translocation programmes.

As was the case for multistate capture–recapture models, the original multistate occupancy models (e.g. Royle 2004; Royle and Link 2005; Nichols et al. 2007; MacKenzie et al. 2009) assume that at least one state is assigned with no uncertainty. For example, if at least one host organism is detected in a sample unit and diagnosed as containing the pathogen, then the unit is assumed to be in state D with certainty. However, laboratory diagnostics are not always perfect, leading to the possibility of both ‘‘false negatives’’ (nondetection) and ‘‘false positives’’ (misclassification), where the latter is an important case of state uncertainty. McClintock et al. (2010) noted this possibility in disease monitoring and emphasized the importance of developing models that incorporate this kind of uncertain state assignment. Occupancy models permitting false positives were first considered by Royle and Link (2006) who presented a very general model. Miller et al. (2011, 2013) extended this general model to incorporate ancillary information (subsets of data for which truth is known) and permit inference when not only false negatives (nondetection) but also false positive misclassification is possible. Chambert et al. (2015) presented basic likelihoods for other kinds of designs providing ancillary data. In particular, their ‘‘calibration design’’ uses diagnostic test data collected on a subset of animals of known disease state as a means of estimating misclassification probabilities, and thus both occupancy state variables and vital rates from disease survey data. Models for some of these designs have already been incorporated into programme PRESENCE (Hines 2006), and the remaining designs will be incorporated shortly. We expect these misclassification models of occupancy dynamics to see increasing use in spatial epidemiology.

Summary and Conclusions

There is an extremely large number of ways to monitor any ecological system. Guidance on which approaches to monitoring are likely to be most useful comes directly from answers to the ''why'' question: exactly what question or decision is the monitoring to inform? When monitoring is to inform conservation decisions, resulting data are typically used to make state-dependent decisions, to assess progress towards programme objectives, to learn in order to make better decisions in the future, and to provide parameter estimates for process modelling. With these specific roles in mind, decisions about what and how to monitor become much easier.

In this paper, we have considered conservation translocation programmes designed to introduce or translocate animals to locations where they are either absent or present in reduced numbers. A natural concern in such programmes is the potential for introducing disease. We focused primarily on the potential for translocated animals to introduce disease to wild animals in natural systems. However, we also noted the possibility of increased susceptibility of translocated animals to disease in natural systems, influencing the success of conservation translocation programmes. Although we did not provide detailed lists of decisions to be informed, we tried to provide guidance by describing generic classes of decisions that might be informed by monitoring at different stages (e.g. pre-release and post-release) of the conservation translocation programme.

Selection of state variables and vital rates to be monitored is then based on the specific decisions that they are intended to inform. Identification of the quantities to monitor is followed by selection of specific field and analytic methods to provide estimates. Sources of variation in field data collection that are important for inference are geographic variation in quantities of interest and detection probability. For the purpose of inference about disease dynamics, both state variables and vital rates are likely to be specific to disease states, such as those of the SIR models. Inference methods must thus be able to deal with uncertainty of state assignment and thus with misclassification of disease state.

The class of inference model needed to inform decisions about disease management and risk will likely vary depending on the decision to be informed. Many decisions will be focused on disease dynamics at the local area of release. Monitoring to inform these decisions can be based on multistate capture–reencounter studies of marked individuals. These models permit inferences about state-specific survival rates and rates of transition between different states (e.g. susceptible to infected), key vital rates governing disease dynamics and effects. The models also permit inferences about state-specific abundances of animals. Other decisions require occupancy models of spatio-temporal dynamics over larger geographic scales. These occupancy models permit inferences about transition probabilities associated with changes of state (e.g. disease absent to disease present) in a location as well as the fraction and number of locations in each disease state.

In summary, monitoring is not an inherently useful endeavour. Rather, it attains utility as a component of a larger process (science, conservation), and its value is determined by its effectiveness in informing the parent process. Translocation of animals is a conservation action that requires making decisions in order to best achieve programme objectives. Objectives of such programmes usually include minimization of disease risk for wild animals in the local area to which animals are being translocated, as well as minimization of disease effects on translocated animals themselves. Here we have described the general decisions that can be informed by disease monitoring within translocation programmes, as well as classes of field methods and associated models that can be used to obtain these inferences. Development of monitoring to serve a specific translocation programme will entail tailoring these general ideas to meet specific needs.

Acknowledgments

We thank the organizing committee of the Health and Disease in Translocated Wild Animals Symposium by the Zoological Society of London (Tony Sainsbury, Katherine Walsh, Ian Carter, John Ewen, and Matt Hartley) for the invitation to prepare this manuscript. We also thank several colleagues for insightful discussions about wildlife disease management and monitoring, including Sarah Converse, Evan Cooch, Joanne Earnhardt, Chris Franson, Robert Gerlach, Bruce Rideout, and Ted Swem. Funding for TEH was provided by the US Fish and Wildlife Service.

References

Adams MJ, Chelgren ND, Reinitz D, Cole RA, Rachowicz LJ, Galvan S, et al. (2010) Using occupancy models to understand

the distribution of an amphibian pathogen, *Batrachochytrium dendrobatidis*. *Ecological Applications* 20:289–302

Arnason AN (1972) Parameter estimates from mark-recapture experiments on two populations subject to migration and death. *Researches on Population Ecology* 13:97–113

Arnason AN (1973) The estimation of population size, migration rates and survival in a stratified population. *Researches on Population Ecology* 15:1–8

Bailey LL, MacKenzie DI, Nichols JD (2014) Advances and applications of occupancy models. *Methods in Ecology and Evolution* 2014:1269–1279

Bled F, Nichols JD, Altwegg R (2013) Dynamic occupancy models for analyzing species' range dynamics across large geographic scales. *Ecology and Evolution* 2013:4896–4909

Bled F, Royle JA, Cam E (2011) Hierarchical modeling of an invasive spread: the Eurasian Collared-Dove *Streptopelia decaocto* in the United States. *Ecological Applications* 21:290–302

Brownie C, Hines JE, Nichols JD, Pollock KH, Hestbeck JB (1993) Capture–recapture studies for multiple strata including non-Markovian transition probabilities. *Biometrics* 49:1173–1187

Chambert T, Miller DAW, Nichols JD (2015) Modeling false positive detections in species occurrence data under different study designs. *Ecology* 96:332–339

Choquet R, Rouan L, Pradel R (2009) Program E-SURGE: a software application for fitting multievent models. In: *Modeling Demographic Processes in Marked Populations, Environmental and Ecological Statistics Series*, Vol 3, Thomson DL, Cooch EG, Conroy MJ (editors), New York: Springer, pp 845–866

Conn PB, Cooch E (2009) Multistate capture–recapture analysis under imperfect state observation: an application to disease models. *Journal of Applied Ecology* 46:486–492

Cooch EG, Conn PB, Ellner SP, Dobson AP, Pollock KH (2012) Disease dynamics in wild populations: modeling and estimation: a review. *Journal of Ornithology* 152(Supplement 2):S485–S509

Eaton MJ, Hughes PT, Hines JE, Nichols JD (2014) Testing metapopulation concepts: effects of patch characteristics and neighborhood on occupancy dynamics of an endangered lagomorph. *Oikos* 123:662–676

Elmore SA, Huyvaert KP, Bailey LL, Milhous J, Alisauskas RT, Gajadhar AA, Jenkins EJ (2014) *Toxoplasma gondii* exposure in arctic-nesting geese: a multi-state occupancy framework and comparison of serological assays. *International Journal for Parasitology: Parasites and Wildlife* 3:147–153

Faustino CR, Jennelle CS, Connolly V, Davis AK, Swarthout EC, Dhondt AA, Cooch EG (2004) *Mycoplasma gallisepticum* infection dynamics in a house finch population: seasonal variation in survival, encounter and transmission rate. *Journal of Animal Ecology* 73:651–669

Gomez-Dias E, Doherty PF, Duneau D, McCoy KD (2010) Cryptic vector divergence masks vector-specific patterns of infection: an example from the marine cycle of *Lyme borreliosis*. *Evolutionary Applications* 3:391–401

Hines JE (2006) PRESENCE-Software to Estimate patch occupancy and related parameters. USGS-PWRC. http://www.mbr-pwrc.usgs.gov/software/presence.html

Jennelle CS, Cooch EG, Conroy MJ, Senar JC (2007) State-specific detection probabilities and disease prevalence. *Ecological Applications* 17:204–267

Johnson FA, Williams BK, Nichols JD, Hines JE, Kendall WL, Smith GW, Caithamer DF (1993) Developing an adaptive management strategy for harvesting waterfowl in North America. *Transactions of the North American Wildlife and Natural Resources Conference* 58:565–583

Kendall WL, Hines JE, Nichols JD (2003) Adjusting multi-state capture–recapture models for misclassification bias: Manatee breeding proportions. *Ecology* 84:1058–1066

Kendall WL, Langtimm CA, Beck CA, Runge MC (2004) Capture–recapture analysis for estimating manatee reproductive rates. *Marine Mammal Science* 20:424–437

Kendall WL, Nichols JD (2002) Estimating state-transition probabilities for unobservable states using capture–recapture/resighting data. *Ecology* 83:3276–3284

Kendall WL, Nichols JD, Hines JE (1997) Estimating temporary emigration and breeding proportions using capture–recapture data with Pollock's robust design. *Ecology* 78:563–578

Kermack W, McKendrick AG (1927) A contribution to the mathematical theory of epidemics. *Proceedings of the Royal Society of London, Series A* 115:700–721

Kery M, Schaub M (2012) *Bayesian population analysis using WinBUGS: a hierarchical perspective*, Amsterdam: Elsevier

Lachish S, Gopalaswamy AM, Knowles SCL, Sheldon BC (2012) Site-occupancy modeling as a novel framework for assessing test sensitivity and estimating wildlife disease prevalence from imperfect diagnostic tests. *Methods in Ecology and Evolution* 3:339–348

Lachish S, Jones M, McCallum H (2007) The impact of disease on the survival and population growth rate of the Tasmanian devil. *Journal of Animal Ecology* 76:926–936

Lancia RA, Nichols JD, Pollock KH (1994) Estimating the number of animals in wildlife populations. In: *Research and Management Techniques for Wildlife and Habitats*, Bookhout T (editor), Bethesda, MD: The Wildlife Society, pp 215–253

Lebreton J-D, Nichols JD, Barker R, Pradel R, Spendelow J (2009) Modeling individual animal histories with multistate capture–recapture models. *Advances in Ecological Research* 41:87–173

MacKenzie DI, Nichols JD, Lachman GB, Droege S, Royle JA, Langtimm CA (2002) Estimating site occupancy when detection probabilities are less than one. *Ecology* 83:2248–2255

MacKenzie DI, Nichols JD, Royle JA, Pollock KH, Bailey LL, Hines JE (2006) *Occupancy Modeling and Estimation*, San Diego, CA: Academic Press, pp 324

MacKenzie DI, Nichols JD, Seamans ME, Gutierrez RJ (2009) Dynamic models for problems of species occurrence with multiple states. *Ecology* 90:823–835

McClintock BT, Nichols JD, Bailey LL, MacKenzie DI, Kendall WL, Franklin AB (2010) Seeking a second opinion: uncertainty in wildlife disease ecology. *Ecology Letters* 13:659–674

Miller DAW, Nichols JD, Gude JA, Rich LN, Podruzny KM, Hines JE, Mitchell MS (2013) Determining occurrence dynamics when false positives occur: estimating the range dynamics of wolves from public survey data. *PLoS One* 8(6):e65808 . doi:10.1371/journal.pone.0065808

Miller DA, Nichols JD, McClintock BT, Grant EHC, Bailey LL, Weir L (2011) Improving occupancy estimation when two types of observational error occur: nondetection and species misidentification. *Ecology* 92:1422–1428

Miller DAW, Talley BL, Lips KR, Grant EHC (2012) Estimating patterns and drivers of infection prevalence and intensity when detection is imperfect and sampling errors occurs. *Methods in Ecology and Evolution* 3:805–859

Murray KA, Skerratt LF, Spear R, McCallum H (2009) Impact and dynamics of disease in species threatened by the amphibian

chytrid fungus, *Batrachochytrium dendrobatidis*. *Conservation Biology* 23:1242–1252

Nichols JD (2001) Using models in the conduct of science and management of natural resources. In: *Modeling in Natural Resource Management: Development, Interpretation and Application*, Shenk TM, Franklin AB (editors), Washington, DC: Island, pp 11–34

Nichols JD, Armstrong DP (2012) Monitoring for reintroductions. In: *Reintroduction Biology: Integrating Science and Management*, Ewen JG, Armstrong DP, Parker KA, Seddon PJ (editors), Wiley-Blackwell: Oxford, pp 223–255

Nichols JD, Hines JE, MacKenzie DI, Seamans ME, Gutierrez RJ (2007) Occupancy estimation with multiple states and state uncertainty. *Ecology* 88:1395–1400

Nichols JD, Williams BK (2006) Monitoring for conservation. *Trends in Ecology and Evolution* 21:668–673

Ozgul A, Oli MK, Boker BJ, Perez-Hyedrich C (2009) Upper respiratory tract disease, force of infection, and effects on survival of gopher tortoises. *Ecological Applications* 19:786–798

Pollock KH (1982) A capture–recapture design robust to unequal probability capture. *Journal of Wildlife Management* 46:752–757

Pradel R (2005) Multievent: an extension of multistate capture–recapture models to uncertain states. *Biometrics* 61:442–447

Royle JA (2004) Modeling abundance index data from anuran calling surveys. *Conservation Biology* 18:1378–1385

Royle JA, Dorazio RM (2008) *Hierarchical Modeling and Inference in Ecology*, New York: Academic Press

Royle JA, Link WA (2005) A general class of multinomial mixture models for anuran calling survey data. *Ecology* 86:2505–2512

Royle JA, Link WA (2006) Generalized site occupancy models allowing for false positive and false negative errors. *Ecology* 87:835–841

Schwarz CJ, Schweigert JF, Arnason AN (1993) Estimating migration rates using tag-recovery data. *Biometrics* 49:177–193

Senar JC, Conroy MJ (2004) Multi-state analysis of the impacts of avian pox on a population of serins (*Serinus serinus*): the importance of estimating recapture rates. *Animal Biodiversity and Conservation* 27:133–146

Skellam JG (1951) Random dispersal in theoretical populations. *Biometrika* 38:196–218

Thompson SK (2002) *Sampling*, *2nd ed.*, New York: Wiley

White GC, Burnham KP (1999) Program MARK: survival estimation from populations of marked animals. *Bird Study* 46:S120–S139

Williams BK, Nichols JD, Conroy MJ (2002) *Analysis and Management of Animal Populations*, San Diego, CA: Academic Press

Yackulic CB, Reid J, Davis R, Hines JE, Nichols JD, Forsman E (2012) Neighborhood and habitat effects on vital rates: expansion of the barred owl in the Oregon Coast Ranges. *Ecology* 93:1953–1966

Yoccoz NG, Nichols JD, Boulinier T (2001) Monitoring of biological diversity in space and time. *Trends in Ecology and Evolution* 16:446–453