Measuring conservation effectiveness:

Occupancy-related metrics for wildlife

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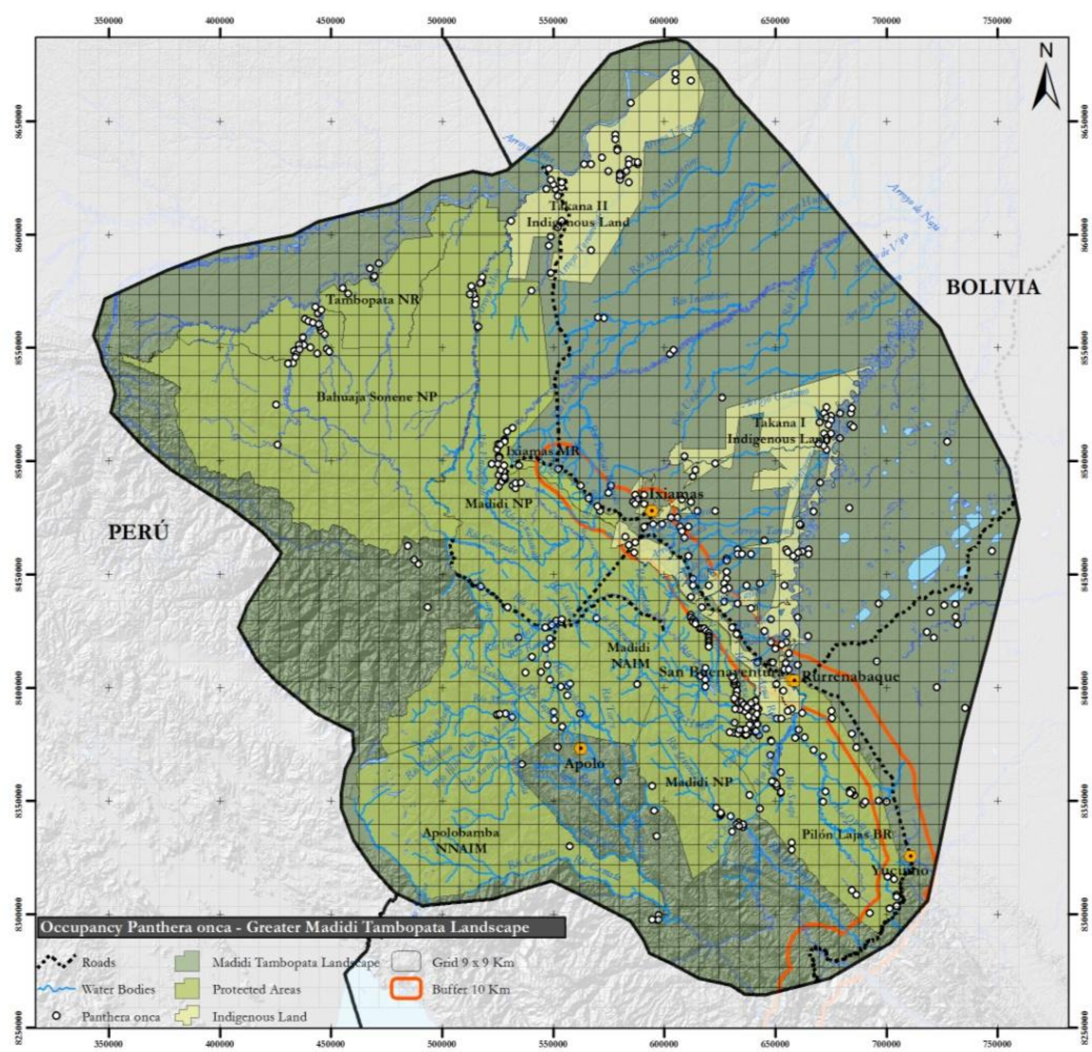

Bolivian portion of Greater Madidi-Tambopata Landscape with 81 km^2 Occupancy Analysis Cell Design for Jaguar

Acknowledgements: Our sincere thanks go to Jim Nichols, Steve Zack, Aaron MacNeil, Andrés Novaro, Arjun Gopalaswamy, and Rob Wallace for their participation in the August 2012 workshop, as well as their additions and suggestions for improvements to this document.

EXECUTIVE SUMMARY

WCS Global Conservation Program is exploring the development of measures of conservation effectiveness focusing on how WCS management interventions affect wildlife populations, wildlife habitat, threats to wildlife and law enforcement effectiveness, natural resource governance, and livelihoods. Here we report on a two-day internal workshop in August 2012, where we invited WCS staff and friends with expertise in occupancy analysis and monitoring to examine the use of occupancy as a metric for within and cross-site comparisons of conservation effectiveness in WCS programs. Occupancy methods are potentially efficient in terms of their application across large areas and the ability to combine multiple sources of information, while providing a scientifically defensible metric of the proportion of a landscape of interest that is occupied. Occupancy-based analyses also can yield information on species richness, relative abundance, and dynamics of species and communities; explanatory variables for detectability and occupancy can be included during analysis. In addition, the results of occupancy analyses can be displayed in a spatially explicit manner, which permits conservation decision makers or donors to easily visualize how conservation management is influencing the status of conservation targets in space and time.

This document highlights some of the key results of the meeting, as well as provides a background to the uses of occupancy analysis in a variety of landscape contexts. In the appendices we give an overview of occupancy methods and a bibliography of recent uses of occupancy models for a variety of taxa.

- We agreed that WCS should use unbiased estimates of occupancy, abundance, density or relative abundance whenever possible.
- We reached a broad consensus that occupancy will be a useful metric for comparing landscape/seascape level wildlife trends between sites and over time.
- We also recognized the limitations of occupancy to provide information on certain kinds of species that are important to our landscapes and seascapes.
- We did not suggest that occupancy be the only metric of conservation effectiveness or that current best practices be abandoned in favor of occupancy.
- We recognized that many interventions are indirect and often we are not the management authority in our Scapes. Under these circumstances, it may be hard to attribute changes in target species abundance and occupancy to our intervention efforts.
- We concluded that occupancy would be a useful metric for the majority of target species in the WCS landscape and seascape portfolio.
- We suggested four activities to move forward on the use of occupancy as a WCS landscape monitoring metric:
    1. Investigate retro-fitting occupancy analyses to current sampling designs and datasets.
    2. Encourage collaboration within and among Regional Programs to increase the power of their monitoring programs by standardizing monitoring data (The development of the camera trap database is a start).
    3. A series of workshops at NCEAS under the NCEAS/TNC/WCS NATURELAB program to investigate structured decision making, monitoring, and assessment of conservation effectiveness in WCS Scapes.
    4. Development of test landscapes in each region (NA, LA, Asia, Africa, Marine) where we engage in occupancy analyses to establish the utility of the efforts.

INTRODUCTION

Results-based management

Within WCS, we advocate the practice of results-based management. This is the process by which, given a management action, we measure effectiveness and adapt project strategies as we learn what does and does not work in promoting conservation. The keys to results-based management are 1) Use of conceptual models to make explicit a results-chain that specifies causal connections between our measurable objective, the direct and indirect barriers that presently prevent us from achieving our objectives and the strategies that we will deploy to take down these barriers; and 2) monitoring how well we implement our chosen strategies, tracking whether threats and barriers are being abated and overcome, and assessing whether the status of our conservation and development targets (our objectives) is improving, declining or static.

By monitoring at three levels - Strategies (also called activities, management or interventions), Threats (and threat reduction) and Targets (wildlife populations response to strategies), we can assess the effectiveness of our investments and adapt our strategies as we learn what works and as the situation changes Strindberg and O'Brien 2012). Thus, we need to be able to track the status of our principal conservation targets, the wildlife species we care about, habitats and threats, as well as additional information that is of perennial interest to major donors**.** At the same time we want to keep our measures to a minimum because there is a strong inverse relationship between the number of indicators to be measured and the probability that they will be measured well.

In selecting impact measures we need to ensure that: 1. they are perceived as transparent and credible (i.e., reported results will be believed); 2. they can be collected at modest additional cost; and 3. they are able to show change over a relatively short time frame.
Recently, WCS Conservation Support was asked to develop a set of impact measures to assess the conservation impact of WCS in its entirety.

The WCS Conservation Assessment Dashboard

We are proposing a five measure dashboard to aggregate information from our landscapes, seascapes, and species programs in an effort to assess and report the conservation impact of our organization as a whole. The dashboard will have the capacity to track changes in our conservation targets (wildlife), their habitat, level of threats, law enforcement effectiveness, natural resource governance, and livelihoods[1].

We propose to produce a graphical WCS Conservation Assessment on programs.wcs.org that provides a measure of our global impact. The Assessment will report a standard set of terrestrial and marine impact measures at each of our 74 landscapes and seascapes, as well as for our Species Programs (clearly Scapes or Species Programs may choose to measure a broader range of factors). The Assessment will be presented as simple, time-series graphs for each individual landscape and seascape (by clicking on a map) and provide a global assessment by aggregating data across landscapes and seascapes, or Species

[1] We include livelihoods because we believe that most poor rural families are dependent on direct use of natural resources for subsistence and income, and thus improvement in the status of targets, habitat, threats and governance should be reflected in improvement in livelihoods. Assessing livelihoods of resource dependent families is, in effect, an aggregate measure of conservation effectiveness.

Program elements. Audiences for this Assessment include the Board of Trustees, all NY and field staff at WCS, donors, other conservation NGOs, and the general public.

The Conservation Assessment will do two important things for WCS:

1) Provide a regular, publicly available, accounting of WCS conservation achievements, reinforcing our position as the most effective, science-based, global conservation NGO;
2) Be the guiding impetus, within our organization, for putting in place the systems needed to more easily and more precisely track, analyze and report our conservation effectiveness.

These measures will be built on the best science and practice available, based on what we are already doing, to ensure that we measure changes that result from our interventions.
Five teams have been put together to develop each of the measures. The remit of each team is to produce the following outputs by 31, December 2012: 1. An analysis of a method or comparable methods that would be deployed across all our Scapes and Species Programs to produce the measure (keeping in mind that the measure needs to be inexpensive but credible, with the premise that less is more because complicated systems are likely to be too costly to implement across appropriate time scales in order to establish and observe trends); 2. Technical guidance for deploying the method or methods within our Scapes and Species Programs; 3. Characterization of a data visualization approach that would make the results of our measures monitoring efforts readily understandable to both a lay and professional audience, and make clear the trends in the measures over time.

In this document, we focus on the progress made in developing a measure to track changes in our conservation targets (wildlife). We convened a workshop to examine the use of occupancy methods as a wildlife metric for within and cross site comparisons of conservation effectiveness in WCS programs. Occupancy methods were considered due to their statistical rigor, potential efficiency of application across large areas and the ability to combine multiple sources of information. They also provide a measure that is of interest for wildlife targets: their changing distribution across the landscape or seascape.

The Workshop

The Occupancy metrics workshop was convened on 2-3 August 2012 to examine the use of occupancy methods as a metric for within and cross-site comparisons of conservation effectiveness in WCS programs. Occupancy may be used to ask questions about whether our interventions have an effect on the target species we care about. Because it explicitly addresses detectability of target species, occupancy provides an unbiased estimate of the proportion of a landscape that is occupied by a species of interest, and is thus an indicator of species distribution, which together with species abundance form the core of target population-level responses to conservation actions. Occupancy-based analyses also can yield information on species richness, relative abundance, meta-population dynamics, dynamics of species and communities. Explanatory variables, or covariates, can also be incorporated in the estimation of occupancy and detection probability allowing us to test hypotheses about interventions and to explore factors that affect occupancy.

Workshop participants were chosen for their expertise in statistics and occupancy analysis (Jim, Aaron, Arjun, Samantha, Tim) and for their interest and experience in landscape monitoring (David, Steve, Rob, Andrés).

David Wilkie: Director, Conservation Support
Jim Nichols: Senior Scientist, Patuxent Wildlife Research Center, U.S. Geological Survey
Tim O'Brien: Senior Scientist, Conservation Support
Samantha Strindberg: Associate Conservation Statistician, Conservation Support
Steve Zack: Senior Conservationist, Coordinator Bird Conservation, Species Conservation Program
Rob Wallace: Conservation Scientist, Latin America Program
Andrés Novaro: Conservation Scientist, Latin America Program
Arjun Gopalaswamy: PhD Student, Oxford University
Aaron MacNeil: Research Scientist, Australian Institute of Marine Science

We were tasked with reaching a conclusion on the following issues:

1. Consensus on an occupancy metric(s) for within and cross-site comparisons;
2. Agreement on methods for relating occupancy metrics to threats and interventions;
3. A clear understanding of the use of covariates in occupancy modeling and how covariates might be standardized across sites;
4. How changes in occupancy relate to changes in abundance and the strength of the relationship.

We agreed that abundance and distribution are the two most important state variables we can use to measure the state of wildlife populations and the impact of WCS interventions. We recognized the value (and challenge) of developing unbiased abundance or relative abundance estimates for parts of large landscapes. We reached a broad consensus that occupancy will be a useful metric for comparing landscape level trends between sites and over time, not just because it may be more feasible sometimes to measure distribution than abundance, but also because of the intrinsic value of having an indicator of the distribution of the target species across the landscape. We also recognized the limitations of occupancy to provide information on certain kinds of species that are important to our landscapes and seascapes. We puzzled over how occupancy relates to the status of extremely rare species, migratory species, nomadic species, and especially pelagic species that may range beyond the bounds of the Scapes or range across such vast areas that we might never be able to afford to achieve adequate coverage to make meaningful inferences. Finally, we recognized that many interventions are indirect and often we are not the management authority in our Scapes. Under these circumstances, it may be hard to attribute changes in target species abundance and occupancy to our intervention efforts. Nonetheless, we concluded that occupancy would be a useful metric for the majority of target species in the WCS landscape and seascape portfolio. We noted that the focus would be on monitoring within Scapes, which might capture some elements of a more comprehensive monitoring program required for tracking the status of conservation targets within the Species Program. Below we summarize our discussions and present some ideas for moving forward with measuring the effectiveness of WCS interventions in our conservation Scapes in terms of a wildlife metric.

Occupancy and Abundance for Conservation Monitoring

The extent of area occupied by a species is an important state variable for conservation. IUCN uses changes in area of occurrence and distribution to guide the listing and change of status of species in the Red List and the USGS uses occupancy in several national and regional monitoring programs. A few definitions are useful to guide our thoughts about occupancy.

Occupancy is the proportion of a region (landscape, study area) that is occupied and can be thought of as the range of the species in the region. Abundance can be expressed as the sum of all patch-specific densities across a region. A species can be present and observed in a sampling unit, present and not observed in a sampling unit or absent from the sampling unit. The more individuals that occur in a sampling unit, the more likely the species will be detected during a sample survey. In IUCN-speak the range of a species is described by the Extent Of Occurrence (EOO – the minimum convex polygon that includes all of the area of normal (or likely) occurrence) and Area Of Occupancy (AOO – the area where the species actually occurs).

Most agree that the positive relationship between occupancy and abundance is real and not a statistical artifact. First, the relationship between AOO and abundance is always positive because zero abundance equals zero AOO and increases from there. Second, a number of studies have shown that species undergoing changes in abundance exhibit a concurrent change in AOO. This principle underlies the use of occupancy as a surrogate for abundance in IUCN Red Lists, setting harvest rates in fisheries and tracking extinction risk and invasive species in conservation biology. Basically as a species' abundance declines, its AOO shrinks, and as a species' abundance increases, its AOO can be expected to increase.

The strength of AOO-abundance relationship, however, is not linear, is scale dependent, being affected by the size of the study area, the size of the sampling unit and in our case, can be species- and context-specific. The linearity of the relationship decreases as the size of the sampling unit increases; for a given abundance, the AOO often increases with sampling unit size; variance in AOO increases with size of sampling unit and size of the study area. We can envision why these relationships hold. Consider a rare exploited species that is suddenly well-protected. In a study area of s potential sampling units, the species occurs in some number of sampling units (s_o) out of the total study area. As it recovers abundance grows first in the occupied sampling units, then the species disperses into unoccupied sampling units. So a lag may occur between increases in abundance and the AOO of the species. As the species continues to increase in abundance, it fills the study area and AOO reaches an asymptote, even though the population may continues to increase. For a given species, as the sampling unit size increases, it may take longer to observe dispersal into unoccupied cells, but it may becomes easier to detect the species within a sampling unit, if more individuals result in a more even distribution across the sampling unit. Therefore, in any monitoring effort using occupancy as a metric, special attention must be paid to issues of scale of movements and home range size in relation to the size of the landscape. Clearly whether the species of interest is territorial or not plays a key role in the relationship between occupancy and abundance, as does the aggregating characteristics of the species with increasing group size weakening the relationship between occupancy and abundance.

Traditionally, ecologists considered the AOO as the proportion of sampling units in a study area where at least one individual was present in a sampling unit. This ignored the state of present but not detected during the sampling effort (detection was assumed to be perfect), and led to estimates of AOO that were biased low because present but not detected cells were lumped with absent cells. To correct the bias, we must estimate the probability p that, if at least one individual is present, it will be detected. Replicated sampling (multiple observers, temporal replication, or spatial replication) allows us to estimate p and correct s_o to obtain an unbiased estimate of AOO, which is represented by the symbol ψ, the probability that a sampling unit is occupied or the proportion of the study area that is occupied.

Methods are available that allow us to estimate p and ψ simultaneously in a maximum likelihood or Bayesian framework. The basic sampling scheme involves multiple visits to all sampling units or a randomly selected subset of potential sampling units in a Scape. Detection/non-detection data are collected during each visit. The sampling is conducted during a time interval short enough that the occupancy state of each sampling unit remains unchanged (the population is closed to change). We also assume that the sampling units and detections are independent. This means that sampling in unit 1 does not affect sampling in unit 2 and that a detection in unit 1 does not change the likelihood of a detection in unit 2. It also means that a detection in unit 1 does not affect the likelihood of subsequent detections in unit 1 (though we have methods to handle with spatial autocorrelation). Furthermore, we assume that species are not misidentified and that occupancy and detection are constant across all sites or that heterogeneity in either detectability, occupancy or both can be modeled with covariates. Fortunately, models exist within the occupancy framework that allow us to relax many of these assumptions.

If we extend this idea to a monitoring framework we would revisit the sampling units over some time interval t. At t_0 and t_1, we would estimate occupancy. During the secondary sampling period within each primary sampling period, occupancy states of each sampling unit remain constant. Between primary sampling periods, occupancy states may change. Occupied sites may become unoccupied (local extinction or ε) and unoccupied sites may become occupied (local colonization or γ). Colonization and extinction are the dynamic parameters (also called vital rates) for the state variable occupancy. The change in occupancy between time 0 and time 1 can be described by the relative effect of γ and ε on ψ_0: $\psi_1 = \psi_0(1 - \varepsilon) + \gamma(1 - \psi_0)$. Conservation interventions affect occupancy over time through their effects on local colonization and extinction.

The strength of occupancy as a monitoring metric is that we can model occupancy, colonization, extinction and detection as functions of covariates. For example, if we are estimating occupancy in a landscape that consists of 4 management regimes that might affect the presence of a target species, we can incorporate “management regimes” as a covariate to estimate the impact of management types on occupancy of the target species. Models incorporating different covariates represent competing hypotheses about factors believed to affect occupancy, colonization and extinction. Over time, multi-year models can be used to evaluate the effectiveness of conservation interventions.

Flavors of Occupancy

There is a wide range of questions and models that can be applied in the occupancy framework (see Appendix 1). In addition to the single season and multi-season occupancy models discussed above, we briefly describe four types of models that may be of interest to WCS for monitoring in wildlife in our Scapes. A recent bibliography of published research using occupancy analyses is included in Appendix 2. Most of the occupancy models can be analyzed in a maximum likelihood or a Bayesian framework.

<u>Species richness models</u>: If our conservation targets include communities of species, one metric of interest is how species richness or the number of species present in our Scape, is changing over time or remaining constant as the result of interventions.

<u>Repeated count models</u>: Occupancy based abundance estimation procedures used to estimate the number of individuals at a point when individuals cannot be identified or marked. Rather than using species presence-absence (detection-nondetection) data, these models are based on counts of individuals

obtained at replicate visits. These can be very useful when the sample sites are discrete (i.e. ponds or woodlots) and where the area of sampling can be defined (i.e. fixed distance point count).

Abundance-induced heterogeneity models: Similar to repeated count models but are based on the idea that heterogeneity in abundance generates heterogeneity in detection probability across the Scape. Uses detection/non-detection data to estimate point abundance, and estimates occupancy as a function of point abundance.

Multi-state models: These models are used when we are interested in not only whether a site is occupied, but whether there are different states that the occupied sites might attain. Two examples might be occupancy with breeding and non-breeding birds, or relative abundance surveys that classify occupancy as none, rare, common, and abundant. These analyses move closer to the kind of monitoring that has relevance for traditional WCS monitoring programs. Multi-state models may be run for multiple seasons to assess questions of change in the state of the population over time.

WCS monitoring and decision making in the face of uncertainty

Jim Nichols gave a thoughtful talk on monitoring for structured decision making in the face of uncertainty. He pointed out that we always have uncertainty about how to manage our Scapes. This uncertainty arises from a lack of understanding of the ecological processes that affect our Scapes (energy flow for example), environmental variation (Climate change), partial control, either due to lack of management authority, or lags in response to intervention, and imperfect observation of the state of nature. Jim argues that well-designed monitoring systems should be able to identify uncertainty and allow us to: 1. Act conservatively when uncertainty is high; and 2. Use knowledge gained in an iterative fashion to reduce uncertainty.

In order to implement a monitoring program using a structured decision making process, we need to follow a series of clear steps, similar to our approaches for Scape conservation planning. First, we need a clear set of objectives regarding what we expect to accomplish. We need a clear set of management alternatives regarding what we are able to accomplish (we are in control) and what we are not able to accomplish (someone else is in control). We need quantitative models to predict the responses to the potential interventions for use in selecting the one that is 'nest' with respect to our objectives. We need a method for determining the credibility of the competing models and an algorithm to identify the optimal decision. Finally, we need a monitoring system to gather data to determine the state of the system and the other relevant variables that affect our conservation targets.

Examples of occupancy-based monitoring in WCS

Tigers Forever: Obtaining baselines for large-scale occupancy by tigers and tiger prey

Spurred by the successes of wild tiger recovery in Nagarahole, India and Sikhote-Alin, Russia, the Tigers Forever program was established by WCS in 2006 with support from Panthera. The goal of Tigers Forever is to increase wild tiger numbers by 50% in ten years in key WCS landscapes across Asia. Following a "source-sink" strategy, each selected landscape consisted of source/potential source sites within a larger sink landscape. The objective was to identify key threats and target interventions at source sites, and document rigorously the recovery of wild tiger numbers. The monitoring strategy involved assessing tiger and prey densities at the source populations annually and assessing the hypothesized "ripple" effect in the larger landscapes using occupancy surveys once every 4-5 years.

The large cell occupancy surveys that employed the Hines et al. (2010) model with spatial replication were used to assess tiger occupancy in the Malenad-Mysore Tiger Landscape in India. The naïve occupancy was found to be 47% lower than the estimated occupancy of 0.66 in this landscape (Karanth et al 2011). The estimated area occupied by tigers was ~14,100 km^2 of the 22,000 km^2 of potential tiger habitat. A similar tiger occupancy survey in Indonesia (Wibisono et al. 2011), but confronted with different models, revealed an estimated occupancy of tigers of 0.70 in comparison to a naïve estimate of 0.52.

Assessment of tiger prey in most source sites in southeast Asia (apart from Huai Kha Kaeng, Thailand, and sites in MMTL, India) posed a major challenge because traditional line-transect surveys were difficult to implement in practice. As an alternative, small cell occupancy surveys were designed to best meet the assumptions of Royle and Nichols (2003) abundance-induced heterogeneity models to estimate large ungulate densities using the field survey protocols of a trial survey in Bhadra (Gopalaswamy et al 2012). Large sample sizes for estimating ungulate prey densities in Malaysia, Laos and Myanmar yielded precise estimates of abundance and occupancy using these models.

Conservation effectiveness of patrolling and law enforcement in BBSNP

Bukit Barisan Selatan National Park (BBSNP) in southern Sumatra, Indonesia was a stronghold for Sumatran tiger, elephant and rhinoceros during the 1990's. In 1995, the International Rhino Program, in collaboration with WWF-Indonesia and PHKA/BBSNP initiated joint patrols in BBSNP. This work was expanded to four patrol units in 1997 to improve coverage of patrols and continues today with 11 patrol units. In 1999, WCS assisted with funding from Save the Tiger Fund. The goal of the armed patrols was to reduce poaching of rhinos, tigers and elephants. In 2003, WCS initiated the Wildlife Crime Unit (WCU) with the objective of filling a capacity gap in being able to respond to and follow up on information regarding poaching of tigers, elephant, rhino and birds at the local and regional level. WCU is an investigation unit that helps the government by supplying the best information on illegal poaching and hunting and also deals with informant networks and promoting public awareness. WCU activities continue today. Between 1998 and 2012, WCS has conducted camera trap surveys throughout the park (1998-2006) and in the southern part of the park (2010-2011), arguably the best zone for wildlife, especially elephant, rhinos and tigers.

To determine whether the interventions (patrols and WCU activity) were effective in reducing poaching and unsustainable hunting, we looked at wildlife trends using the occupancy-based Wildlife Picture Index (WPI: O'Brien et al 2010). We found a park-wide decline in the WPI between 1998 and 2006 suggesting an erosion in biodiversity of medium and large sized mammals. Tigers, elephants and rhinos declined faster than the rate of forest loss and faster than the rate of loss for species that were hunted as crop-raiders or for subsistence. Species hunted for subsistence and persecuted for crop-raiding declined at rates similar to forest loss. Species that had no economic value showed no consistent pattern: declines and increases were balanced.

A more recent analysis looked at trends between 1998 and 2011 in the south of BBSNP, a well-protected area due to patrols, a private concession in the south and the presence of the WCS Way Canguk Research Station. In this area, there was a significant increase in the WPI between 1998 and 2011 for 34 mammal species. Tigers, elephants and rhinos, however, declined over this time period. Thus we conclude that the patrol efforts and WCU efforts may not have been sufficient to stem the loss of the 3 most endangered large mammals in the park.

Effect of livestock management on diversity, distribution and abundance of large mammals in Laikipia County, Kenya.

Successful conservation of large terrestrial mammals on private lands requires that landowners be able to manage wildlife to derive benefits that offset costs of wildlife. In Laikipia County, Kenya (9,666 km^2), all of the wildlife are on private lands, and land use and tolerance attitudes play a major role in the fate of wildlife. Kinnaird and O'Brien (2012) used camera traps to sample large mammal communities to determine the impact of 4 different livestock management systems (rhinoceros sanctuaries: no livestock; conservancies: intermediate stocking rates; fenced ranches and pastoralist group ranches: highest stocking rates) to examine whether management and stocking rates affect wildlife communities. We deployed cameras across 8 properties and used the photographs to estimate species richness in an occupancy framework, species' occupancies, and relative abundances. Species richness was highest on conservancies and sanctuaries, and lowest on fenced and group ranches. Occupancy estimates were, on average, twice as high on sanctuaries and conservancies as on fenced ranches, and five times higher than on group ranches. The relative abundances of most species were highest or second-highest on sanctuaries or conservancies. We identified exclusion fencing and overstocking of sheep and goats as major impediments to wildlife distribution and abundance. But we also found that wildlife thrived under a moderate stocking level that allowed space for wildlife. Kenya's policy toward wildlife is government ownership and no consumptive use. The lack of landowner rights to manage wildlife is therefore a key policy issue to tackle for wildlife conservation in Laikipia. Current policies prevent many direct management options that might improve the situation. Alternatives that are available include applying a landscape-level approach to land use planning that aims to increase the area under conservation by providing incentives for conservation on overstocked and fenced properties.

Modeling Wolverine Occurrence Using Aerial Surveys of Tracks in Snow

Justina Ray and colleagues (Magoun et al. 2007) designed a novel approach to determine the extent of distribution and area of occupancy for wolverines (*Gulo gulo*) by using aerial surveys of tracks in snow and hierarchical occupancy modeling. They used a small, fixed-wing aircraft with pilot and one observer to search 575 of 588 survey units for wolverine tracks in approximately 60,000 km^2 of boreal forest in northwestern Ontario, Canada. They used sinuous flight paths to scan open areas in the forest in the 100-km^2 survey units. They detected tracks in 138 (24%) of the 575 sampled units. There was strong evidence of occurrence (probability of occurrence > 0.80) in 30% of the 588 survey units, weak evidence of occurrence (0.50–0.80) in 12%, weak evidence of absence (0.20–0.50) in 15%, and strong evidence of absence (< 0.20) in 43%. Wolverine range comprised 59% of the study area and area of occupancy was 33,400 km^2. With information on probability of occurrence and core areas of occupation for wolverines in the study area, resource managers and others can examine factors that influence wolverine distribution patterns and use this information to formulate best management practices that will maintain wolverines on the landscape in the face of increasing resource development. Comparing future survey results with those of the 2005 survey will provide an objective way to assess the efficacy of management practices.

Potential of occupancy methods for monitoring rare species in the Andean Patagonian Steppe Landscape

The unique wildlife of the Andean Patagonian Steppe Landscape includes a large (25 kg), flightless bird, the Darwin´s rhea, with populations that have been decimated by hunting, egg collection, and habitat degradation due to livestock grazing and hydrocarbon development. To assess effectiveness of conservation interventions and also learn about the factors that affect rhea distribution, WCS is developing a monitoring system based on an occupancy analysis with a single-season model. Unlike the other large-bodied herbivore in the landscape, the conspicuous guanaco, which is easy to observe and count on transects from vehicles in the open steppe, rheas are in lower densities and harder to observe, although feces can be easily detected in walking transects. A calibration by the WCS team also indicates that fecal counts accurately reflect rhea densities. Based on a pilot survey of 20 transects (where we did repeated surveys throughout the year) we estimated a very high detection rate for rhea feces (83%). Because the portion of the landscape for which we wished to estimate occupancy is very large (>2.5 million hectares) and many areas are difficult to reach, repeated visits in a single season would be prohibitively expensive in both time and money. Therefore, we decided to conduct multiple, 1-km transect surveys on a single visit within each 2 X 2 km area. To design the survey we performed simulation analysis using program PRESENCE, and determined that 100 cells sampled with 2 transects and a sub-sample of 20 cells sampled with 4 transects would be sufficient to estimate occupancy with high precision (SE = 0.04). We overlaid a 2 X 2 km grid over the area, and randomly selected 100 cells which we sampled with transects with randomly selected starting points and orientations within the cell. Sampling was carried out in six 10-13-day campaigns by 3-5 people at total cost of $ 18,000. We estimated detection probability for rheas to be 0.78 (SE = 0.04), and the proportion of sites occupied in the landscape was 0.63 (SE = 0.05). Using logistic regression analysis we evaluated the relationship between rhea presence and elevation, vegetation type, livestock density, road density (including seismic lines for oil exploration that are useable by 4-wheel-drive vehicles), and distance to rural houses (people collect eggs and hunt birds for food). We found that the presence of rheas was negatively affected by elevation and livestock density. We are currently developing a protocol for repeating this survey every 3-5 years to determine changes in rhea occupancy through time and assess success of conservation measures.

Feces of other species of conservation concern can be detected in the walking transects, so we are evaluating the use of this survey technique and design to simultaneously monitor occupancy by the assemblage of large (2-8 kg) hystricomorph rodents. These rodents have more restrictive habitat requirements than rheas, so some adaptation of the sampling scheme will need to be employed. In the case of the guanaco, occupancy surveys may be cheaper to use than line transects used to estimate abundance and sufficient for our monitoring purposes in some portions of the landscape and for evaluating the effects of some interventions or threats. A WCS radiotelemetry study has determined that ca 60% of the large northern guanaco population is migratory, and our transect data over the last 20 years show that social structure is also fluid, with group size and conformation changing seasonally. Therefore, if we decide to employ occupancy analysis as a monitoring technique for guanacos, surveys will need to be conducted at least twice during the year to determine distribution in summer and winter ranges.

Occupancy methods to assess changes in species fish diversity on coral reefs

Surveys for coral reef fishes are frequently conducted using underwater visual census (UVC) methods that use one of two common survey types, line transects or point counts, to take replicate samples from a given reef at a specific point in time. These surveys are often repeated annually, making conventional UVC monitoring a natural fit for species richness occupancy analysis, whereby within-year UVC replicates are capture occasions used to estimate detectability of individual species and the total occupancy of species across the assemblage provides an estimate of species richness. This approach is only just being applied to coral reef ecosystems[2] but a recent application by Cheal et al. (2012) used a hierarchical occupancy model to infer relative functional redundancy of reef fish communities on the Great Barrier Reef (GBR). To do this, Cheal et al. estimated the average probability of occupancy for herbivorous fishes on reefs within management sectors of the GBR. These reef and sector-level estimates represented the average probability of presence for herbivorous fishes, a direct analogue of functional redundancy that was readily comparable among reefs and sectors. Cheal et al. found that inner-shelf reefs, particularly near the cities of Cairns and Townsville, had the lowest functional redundancy across the GBR, potentially an intrinsic pattern of the GBR ecosystem. Importantly the occupancy approach used matched the current long-term sampling scheme for the Australian Institute of Marine Science and should be equally applicable to most reef monitoring programs.

Migratory Species

For migratory species, with life cycle activities often widely separated by geography, the problem at first seems intractable by scale. In the case of migratory birds and many marine mammals, however, most species studied show remarkable site fidelity at both their breeding grounds and (with more spatial variation) in their wintering grounds. Thus there seems to be the opportunity to examine occupancy estimates for populations of such migrants at the ends of their migrations. Hypothetically, such estimates could provide information as to where interventions are most needed. Assessment in passage migration (moving latitudinally or altitudinally) is more problematic, unless the migratory species has few and well known stopover areas (as is true for red knots and their dependence on Delaware Bay in their northward migration from southern Argentina to Arctic Canada). This perspective is all hypothetical, as no migratory species has been assessed by these means to date.

Design considerations for occupancy studies

An occupancy metric is not a panacea for all of the WCS species of interest. As species become more common, often the cost of estimating abundance goes down and the precision increases. At the same time, occupancy analyses are not useful (or interesting) when true occupancy approaches 100%. Occupancy methods perform best when detection is high, occupancy is moderate, and we have many sampling sites. In general assessment of occupancy states and their dynamics seem to work best when the occupancy states are in the range of 0.3 to 0.8. Low detection probabilities can cause problems for occupancy because the estimates become increasingly less accurate as detection probabilities become very small. Thus it is important to maximize detection probabilities, which is a challenge when the study area is largely unknown, although some general rules may apply (e.g., in dry forest pellets work well for

[2] Aaron MacNeil collaborated with Tim McClanahan to apply this approach to the WCS coral reef data from Kenya.

ungulates, in rainy places tracks are better). Increasing the number of sample units and sampling occasions generally increases the accuracy and precision of occupancy estimates. In general, for a rare species it is more efficient to survey more sampling units with fewer replications because we are interested to identify populations of the rare species, while for a common species fewer sampling units should be surveyed with more replicates. In either case, we should always measure meaningful covariates to better understand what drives species occupancy.

Few wildlife species of interest to WCS are likely to be widely distributed on the landscape. Many species will have clumped distribution; some will be widespread but patchy for many reasons. Fortunately, there are a couple of modeling tools to help with designing and evaluating the potential sensitivity of occupancy monitoring programs. Occupancy software PRESENCE includes a simulation routine that allows you to determine the degree of bias and precision likely to occur for a given level of sampling units and sampling effort when estimates or guesses of true occupancy and detection probability are provided. This allows one to quickly evaluate a number of scenarios of sampling effort. For more complex sampling designs, GENPRES software may be used to assist in developing sampling designs. We recommend using GENPRES when designing occupancy studies.

Choice of sites (sampling units, grid cells) is important both for interpretation of occupancy statistics and for cost of sampling design. At the spatial scale of a site, the intent is to infer if the target species is present or absent. By combining data from a number of sites, we calculate the probability of occupancy as a value between 0 and 1. The size of a site is dependent on many factors, including the management objectives for the Scape (and potentially the scale of the threat being mitigated). As discussed earlier, measures of occupancy can be scale dependent, especially for arbitrarily determined sites within contiguous habitat (i.e. sampling grids in forests). A larger site has a higher probability of occupancy than a smaller site. MacKenzie et al. (2006) suggest that a site should be large enough to have a reasonable probability of the species being present, but small enough that the measure of occupancy is meaningful and site can be surveyed in a cost-effective manner. In order to draw inferences about a landscape, sites should be selected using some probabilistic sampling scheme (simple random, stratified random, systematic with random starting site, etc.) unless the entire landscape is sampled. The closure assumption means that either the occupancy state does not change during the sampling period (true occupancy-site is permanently occupied) or that the changes in occupancy within a season are random (use-site is sometimes occupied during the season). This interpretation suggests that the closure assumption may be more easily met for large sites than for small sites.

When designing occupancy over time we need to consider the biological characteristics of the species of interest, as well as how our investments are likely to influence occupancy and over what time frame. This of course becomes more complicated with multiple target species because species-specific landscapes may vary.

Sampling designs are very flexible in occupancy analysis. Sample replication may be spatial or temporal or by means of independent observers. There are three basic sampling strategies: Standard design in which all sites are sampled K times; double sampling design in which a subset of sites is sampled K times and the remaining sites are sampled once; and a removal design in which all sites are sampled up to K times but sampling at a site stops when a target species is detected.

We discussed the problem of misidentification of species due to a variety of causes. Target species may be misidentified in a photograph, or a track or other indirect sign may be wrongly attributed to the target species. Interviews may also lead to misidentification if the interviewee is unsure of when and where he saw a species, or confuses the target species with another species. We discussed a number of methods to control for misidentification of target species, including additional questions to verify truthfulness and accuracy and independent sampling in a selection of sites covered in the context of the sign or interviews surveys. We also discussed the use of mixed methods to increase sample sizes. Mixed methods can be incorporated into a sampling design to yield unbiased estimates of occupancy. For example, we might define sampling units appropriate for jaguar and conduct structured interviews with communities to determine within which of these sampling units community members have observed jaguars within the last three months. We could then visit a subset of the same sampling units identified for the community interview (and possibly visit additional units) and survey for jaguars sign along rivers. As even our field teams might not correctly distinguish jaguar from puma sign, we could also potentially set up a camera trap or DNA-based study to obtain further information to deal with potential misidentification of jaguar. Under either of these sampling schemes, the investigator would visit areas where jaguars were designated as being present as well as areas where jaguar were designated as being absent.

We advocate the balanced use of covariates to model heterogeneity in detection probability and occupancy, and to test hypotheses of interest to monitoring. Covariates may be measured in the field during sampling or may be assigned using global knowledge of the landscape (e.g. GIS information). If covariates are measured in the field, then the inferences using those covariates is strictly valid only for the area sampled because we cannot use the covariates to make predictions about areas not visited. If covariates are assigned based on some global knowledge (land-use, habitat, climate, deforestation), then we can make predictions about expected occupancy of locations within the surveyed area that were not sampled. It is especially important to include covariates that might affect detection probability because the models assume that all heterogeneity in detection is modeled and violation of this assumption can lead to biased inferences. Note that a modeling approach that involves finite mixture models provides an alternative for dealing with potential heterogeneity from an unknown source, i.e. when we do not have the appropriate covariate information. Ignoring covariates that might affect occupancy (e.g. habitat types) will reduce the precision of the estimates but should not induce bias. When evaluating management interventions or conservation effectiveness, we can use stratification of the landscape into treatments and calculate occupancy separately for each treatment then compare results. A more efficient alternative is to treat the interventions as covariates within a single analysis. The nature of the objectives and the data may lend itself to one strategy over the other. For example, if law enforcement is one of our interventions then we could stratify by law enforcement effort, e.g. none, low, medium, high, or alternatively assign a continuous variable value to each of the sampling units.

Way Forward

We found it quite productive to discuss the design and analytical issues for Madidi, Bolivia as a way to move the discussion from the abstract to the realm of possibility. Rob Wallace prepared a companion planning document (Wallace 2012) for implementing an occupancy-based monitoring program in the Madidi Landscape. In addition, we offered several ideas for moving forward with the investigation of the use of occupancy as a conservation effectiveness metric for wildlife:

1. Investigate retro-fitting occupancy analyses to current sampling designs and datasets. Samantha and Boo Maisels are looking at the Central Africa elephant and ape data set to determine if it is appropriate to integrate the traditionally analyzed transect data with both the travel and guided

reconnaissance data (usually not included in analyses due to known sampling biases). This would provide additional spatial coverage and increase sample sizes for species for which estimates can generally not be obtained from the transect data (e.g. forest buffalo, bongo, red river hog, leopard). Margaret Kinnaird, Samantha and Tim have done the same for aerial surveys in Laikipia. Aaron suggested further application of the species richness estimation methods to UVC data to WCS sites in Kenya and elsewhere. A key question that we need to answer is whether designs that maximize detection probability for a single (or few) target species can be used to assess occupancy of non-target species. This is a fundamental question for the utility of large cat monitoring programs for non-target species monitoring, i.e. placing camera traps to detect tigers you may be less likely to detect tiger prey species that avoids tiger trails. Ullas and Arjun are of the opinion that it is not appropriate for the India sites. However, we believe that the results may be biased, but if the bias is consistent, or there are covariates that can be used to address the sampling bias the data may still useful. We need to explore this option further.

2. We need to bring together programs that are interested in increasing the power of their monitoring programs to explore ways to get more from their data – turning by-catch into filets. A first step is to develop a standard database for WCS monitoring data. We recommend that WCS, as part of the TEAM data federation exercise, integrate camera trap and other monitoring data from WCS TEAM sites and two additional Latin America sites into a WCS camera trap database. Partial funding for this may be provided by TEAM.
3. We recommend that WCS engage in a series of workshops at NCEAS under the NCEAS/TNC/WCS NATURELAB program to investigate structured decision making, monitoring, and assessing conservation effectiveness in WCS Scapes.
4. We recommend the development of a test landscape in each region (NA, LA, Asia, Africa, Marine) where we engage in occupancy analyses (either retro-fit or design of new surveys) to establish the utility of the efforts.

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Appendix 1: Brief Overview of Occupancy Methods

Compiled by Tim O'Brien and Samantha Strindberg *March 2012*

Occupancy methods estimate the proportion of a habitat or number of patches occupied when detection is incomplete (Mackenzie et al., 2002, Mackenzie et al., 2003, Mackenzie et al., 2006). When sampling units are scaled to the home range size of target species, the interpretation is proportion of area occupied. When sampling units are smaller than home ranges, the interpretation is intensity of use. The analysis recognizes three states: occupied and species detected, occupied and species not detected, and not occupied. It provides estimates of the probability that a sampling unit is occupied and the probability that at least one individual animal (or sign, if sign surveys are used) is detected. It requires replicated observations on each sampling unit and it allows for covariates that might affect occupancy or detection to be incorporated into the analysis. The basic method assumes demographic and spatial closure during a sampling period (referred to as a season) such that the occupancy status does not change and that sampling units states are independent. Additional assumptions include no errors in identifying species and that observations are independent. There are analysis options that relax most of these assumptions should this be needed. The fundamental reference for occupancy analysis is the MacKenzie et al. 2006 book *Occupancy Estimation and Modeling: Inferring Patterns and Dynamics of Species Occurrence*. The University of Vermont Cooperative Fish and Wildlife Research Unit Spreadsheet Project has an excellent website for self-training in occupancy methods (http://www.uvm.edu/rsenr/vtcfwru/spreadsheets/occupancy.htm). The Patuxent Wildlife Research Center Software page (http://www.mbr-pwrc.usgs.gov/software/doc/presence/ presence.html) also provides a useful user manual that outlines the different analyses available in PRESENCE. Key references for designing occupancy studies include MacKenzie and Royle (2005) and Bailey et al. (2007). The methods are continually evolving and some of the analysis options currently available include:

<u>Single Season models</u> - this is the basic occupancy model, which allows for estimates of the proportion of the study area occupied and the detection probability. Occupancy and detection parameters may be constant across the sampling area or be estimated as a function of site and survey-specific covariates. Single season models based on mixture models to deal with unobservable heterogeneity can also be used. Substitution of species for samples permits estimation of species richness in a study area and exploration of the covariates that affect species richness. When covariates are used to estimate occupancy, predictive maps can be developed to include occupancy estimates for sites in which no detections were made and for sites that were not sampled (but fall within the study area and have covariate data) can be generated. Single season models can also be used for meta-population modeling.

Mackenzie, D.I., Nichols, J.D., Lachman, G.B., Droege, S., Royle, J.A. and Langtimm, C.A. 2002. Estimating site occupancy when detection probabilities are less than one. Ecology 83:2248-2255.

<u>Multi-season models</u> - are an extension of single season models and can be used for inferences about occupancy and meta-population dynamics. Sites can change between being occupied and unoccupied over time allowing for estimates of rates of local extinction and local colonization. Single and multi-season models are ideal for large scale surveys of single species, single populations, meta-populations and communities.

Mackenzie, D.I., Nichols, J.D., Hines, J.E., Knutson, M.G. and Franklin, A.B. 2003. Estimating site occupancy, colonization and local extinction probabilities when a species is not detected with certainty. Ecology 84:2200–2207.

Single season with false positive detections models - are useful when there is a good chance that sign, or aural cues or visual identifications are incorrect. For example, this happens with scat surveys, bird counts using calls, and blurry camera trap photos of duikers and viverrids.

Royle, J.A., Link, W.A. 2006. Generalized site occupancy models allowing for false positive and false negative errors. Ecology 87:835-841.

Miller, DA, Nichols, JD, McClintock, BT, Grant, EHC, Bailey, LL, Weir, LA. 2011. Improving occupancy estimation when two types of observational error occur: non-detection and species misidentification. ECOLOGY 92:1422-1428.

Multi-method models - allow estimation of occupancy when more than one method for detection is employed across sites, providing detection probabilities for each method used. This is useful for hybrid surveys or surveys using multiple cues (e.g., species richness estimation for bird communities using visual and aural cues).

Nichols, J.D., Bailey, L.L., O'Connell, A.F., Talancy, N.W., Grant, E.H.C., Gilbert, A.T., Annand, E.M., Husband, T.P., Hines, J.E. 2008. Multi-scale occupancy estimation and modeling using multiple detection methods. Journal of Applied Ecology 45:1321-1329.

Single season multi-state models - are used when we are interested in not only whether a site is occupied, but whether there are different states that the occupied site might attain (for example occupied with breeders, occupied with non-breeders, or occupied but with different classes of abundance). This can be very important for breeding bird surveys, and for meta-population analyses.

Nichols, J.D., Hines, J.E., MacKenzie, D.I., Seamans, M.E., Gutierrez, R.J. 2007. Occupancy estimation and modeling with multiple states and state uncertainty. Ecology 88:1395-1400.

MacKenzie, D.I., J.D. Nichols, M.E. Seamans, and R.J. Gutierrez. 2009. Modeling species occurrence dynamics with multiple states and imperfect detection. Ecology 90:823–835.

Multi-season multi-state - extend multi-state models to multiple seasons. For example, occupancy models can be used to estimate if a species is *absent*, *rare*, or *abundant* (i.e., 3 population states) or alternatively, if different life history stages are present such as: *absent*, *juvenile*, *adults*. When combined, models can be used to estimate meta-demographic rates such as colonization, extinction, reproduction and recruitment.

MacKenzie, D.I., J.D. Nichols, M.E. Seamans, and R.J. Gutierrez. 2009. Modeling species occurrence dynamics with multiple states and imperfect detection. Ecology 90:823–835.

MacKenzie, D.I., L.L. Bailey, J.E. Hines, and J.D. Nichols. 2011. An integrated model of habitat and species occurrence dynamics. Methods in Ecology and Evolution 2:612-622.

Multi-season integrated habitat occupancy - can be used to examine how habitat suitability and factors that affect habitat suitability can influence the distribution and relative abundance of organisms over time. (This has been used with elephants at water holes in Zimbabwe and would be a good candidate for comparing dung surveys over time).

MacKenzie, D.I., J.D. Nichols, M.E. Seamans, and R.J. Gutierrez. 2009. Modeling species occurrence dynamics with multiple states and imperfect detection. Ecology 90:823–835.

Martin, J, Chamaille-Jammes, S, Nichols, J.D., Fritz, H., Hines, J.E., Fonnesbeck, C.J., MacKenzie, D.I., Bailey, L.L. 2010. Simultaneous modeling of habitat suitability, occupancy, and relative abundance: African elephants in Zimbabwe. Ecological Applications 20:1173-1182.

2 species co-occurrence models - are used when the goal is to determine if 2 species occupy a site, whether occupancy is affected by co-occurrence, and to assess whether they affect each other's detection probabilities. We can also test if the detection probability of one species changes in the presence of the other.

MacKenzie D.I., Bailey, L.L., Nichols, J.D. 2004. Investigating species co-occurrence patterns when species are detected imperfectly. Journal of Animal Ecology 73:546-555.

Repeated count models - are occupancy based abundance estimation procedures used to estimate the number of individuals at a point when individuals cannot be identified or marked. Rather than using species presence-absence (detection-nondetection) data, these models are based on counts of individuals obtained at replicate visits. These can be very useful when the sample sites are discrete (i.e. ponds or woodlots) and where the area of sampling can be defined (i.e. fixed distance point count).

Royle, J.A. 2004. N-Mixture Models for Estimating Population Size from Spatially Replicated Counts. Biometrics 60, 108-115.

Single season heterogeneity models - similar to above but is based on the idea that heterogeneity in abundance generates heterogeneity in detection probability. Uses presence/absence data to estimate point abundance, and occupancy as a function of point abundance.

Royle, J.A., Nichols, J.D. 2003. Estimating abundance from repeated presence-absence data or point counts. Ecology 84:777-790.

Single season staggered entry - are used when we cannot assume that the population is closed within a season. Instead, individuals of the speciees are assumed to arrive and depart from the study area. We estimate P(arrival), P(depature) and P(detection) to develop occupancy estimates.

Kendall, W.L., Hines, J.E,. Nichols, J.D., Grant, E.H. (in prep.) Relaxing the closure assumption in single-season occupancy models: staggered arrival and departure times.

Single season spatial/temporal autocorrelation - occupancy analysis and many other estimation methods assume that detections are independent in space and time. When conducting sign surveys along trails, or using camera traps we may encounter situations where observations are correlated in space or time. These models incorporate autocorrelation in detections to produce unbiased occupancy and detection estimates.

Hines, J.E., Nichols, J.D., Royle, J.A., MacKenzie, D.I., Gopalaswamy, A.M., Kumar, N.S., Karanth, K.U. 2010. Tigers on trails: occupancy modeling for cluster sampling. Ecological Applications 20:1456-1466.

Bled, F. Royle, J.A. and Cam, E. 2011. Hierarchical modeling of an invasive spread: The Eurasian collared-dove *Streptopilia decaocto* in the United States. Ecological Applications 21:290-302.

Occupancy analysis can be carried out in a maximum likelihood (frequentist) framework or a Bayesian framework. The PRESENCE software facilitates frequentist analysis of occupancy data and can be used for single species studies, community level studies and estimation of species richness. It is available as a free download from Patuxent Software Archive (www.mbr.pwrc.usgs.gov/software.html). Occupancy analysis can also be carried out in R using the Unmarked package (http://github.com/rbchan/unmarked).

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Appendix 2: A Short Bibliography of Occupancy Methods Related Publications

Compiled by Tim O'Brien

As part of the WCS Conservation Support work on measures of conservation effectiveness, I compiled a partial list of publications that use occupancy methods. I surveyed Animal Conservation, Auk, Biological Conservation, Bird Conservation International, Conservation Biology, Ecology, Ecological Applications, Herpetologica, Ibis, Journal of Applied Ecology, Journal of Herpetology, Journal of Wildlife Management, and Wildlife Society Bulletin for articles that apply presence/absence and detection/nondetection methods, published between 2002 (first paper by MacKenzie et al. on occupancy analysis) and 2012. Most articles use occupancy-based methods, but allogistic regressions, presence only methods, and incidence functions. I focused on wildlife applications, but there is a wide array of taxa-specific papers included.

METHODS and GENERAL

Aing, C, Halls, S, Oken, K, Dobrow, R, Fieberg, J. 2011. A Bayesian hierarchical occupancy model for track surveys conducted in a series of linear, spatially correlated, sites. JOURNAL OF APPLIED ECOLOGY 48:1508-1517.

Bailey, LL, Hines, JE, Nichols, JD, MacKenzie, DI. 2007. Sampling design trade-offs in occupancy studies with imperfect detection: Examples and software. ECOLOGICAL APPLICATIONS 17:281-290.

Berglund, H, O'Hara, RB, Jonsson, BG. 2009. Quantifying Habitat Requirements of Tree-Living Species in Fragmented Boreal Forests with Bayesian Methods. CONSERVATION BIOLOGY 23:1127-1137.

Bled, F, Royle, JA, Cam, E. 2011. Assessing hypotheses about nesting site occupancy dynamics. ECOLOGY 92:938-951.

Christy, MT, Adams, AAY, Rodda, GH, Savidge, JA, Tyrrell, CL. 2010. Modelling detection probabilities to evaluate management and control tools for an invasive species. JOURNAL OF APPLIED ECOLOGY 47:106-113.

Conroy, MJ, Runge, JP, Barker, RJ, Schofield, MR, Fonnesbeck, CJ. 2008. Efficient estimation of abundance for patchily distributed populations via two-phase, adaptive sampling. ECOLOGY 89:3362-3370.

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Dorazio, RM. 2007. On the choice of statistical models for estimating occurrence and extinction from animal surveys. ECOLOGY 88:2773-2782.

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Ferraz, G, Sberze, M, Cohn-Haft, M. 2010. Using occupancy estimates to fine-tune conservation concerns. ANIMAL CONSERVATION 13:19-20.

Field, SA, Tyre, AJ, Possingham, HP. 2005. Optimizing allocation of monitoring effort under economic and observational constraints. JOURNAL OF WILDLIFE MANAGEMENT 69:473-482.

Fitzpatrick, MC, Preisser, EL, Ellison, AM, Elkinton, JS. 2009. Observer bias and the detection of low-density populations. ECOLOGICAL APPLICATIONS 19:1673-1679.

Gaston, KJ, Fuller, RA. 2009. The sizes of species' geographic ranges. JOURNAL OF APPLIED ECOLOGY 46:1-9

Gormley, AM, Forsyth, DM, Griffioen, P, Lindeman, M, Ramsey, DSL, Scroggie, MP, Woodford, L. 2011. Using presence-only and presence-absence data to estimate the current and potential distributions of established invasive species. JOURNAL OF APPLIED ECOLOGY 48:25-34.

Green, AW, Bailey, LL, Nichols, JD. 2011. Exploring sensitivity of a multistate occupancy model to inform management decisions. JOURNAL OF APPLIED ECOLOGY 48:1007-1016.

Griffin, SC, Taper, ML, Hoffman, R. 2010. Ranking Mahalanobis Distance Models for Predictions of Occupancy From Presence-Only Data. JOURNAL OF WILDLIFE MANAGEMENT 74:1112-1121.

Grouios, CP, Manne, LL. 2009. Utility of Measuring Abundance versus Consistent Occupancy in Predicting Biodiversity Persistence. CONSERVATION BIOLOGY 23:1260-1269.

Gu, WD, Swihart, RK. 2004. Absent or undetected? Effects of non-detection of species occurrence on wildlife-habitat models. BIOLOGICAL CONSERVATION 116:195-203.

Halstead, BJ, Wylie, GD, Coates, PS, Casazza, ML. 2011. Bayesian Adaptive Survey Protocols for Resource Management. JOURNAL OF WILDLIFE MANAGEMENT 75:450-457.

Hodgson, JA, Moilanen, A, Thomas, CD. 2009. Metapopulation responses to patch connectivity and quality are masked by successional habitat dynamics. ECOLOGY 90:1608-1619.

Hui, C, McGeoch, MA, Reyers, B, le Roux, PC, Greve, M, Chown, SL. 2009. Extrapolating population size from the occupancy-abundance relationship and the scaling pattern of occupancy. ECOLOGICAL APPLICATIONS 19:2038-2048.

Johnson, DM. 2005. Metapopulation models: An empirical test of model assumptions and evaluation methods. ECOLOGY 86:3088-3098.

Jones, JE, Kroll, AJ, Giovanini, J, Duke, SD, Betts, MG. 2011. Estimating thresholds in occupancy when species detection is imperfect. ECOLOGY 92:2299-2309.

Jones, JPG. 2011. Monitoring species abundance and distribution at the landscape scale. JOURNAL OF APPLIED ECOLOGY 48:9-13.

Joseph, LN, Field, SA, Wilcox, C, Possingham, HP. 2006. Presence-absence versus abundance data for monitoring threatened species. CONSERVATION BIOLOGY 20:1679-1687.

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Kery, M, Royle, JA, Plattner, M, Dorazio, RM. 2009. Species richness and occupancy estimation in communities subject to temporary emigration. ECOLOGY 90:1279-1290.

Kery, M, Royle, JA, Schmid, H, Schaub, M, Volet, B, Hafliger, G, Zbinden, N. 2010. Site-Occupancy Distribution Modeling to Correct Population-Trend Estimates Derived from Opportunistic Observations. CONSERVATION BIOLOGY 24:1388-1397.

McClintock, BT, Bailey, LL, Pollock, KH, Simons, TR. 2010. Unmodeled observation error induces bias when inferring patterns and dynamics of species occurrence via aural detections. ECOLOGY 91:2446-2454.

MacKenzie, DI. 2005. What are the issues with presence-absence data for wildlife managers? JOURNAL OF WILDLIFE MANAGEMENT 69:849-960.

MacKenzie, DI, Nichols, JD, Lachman, GB, Droege, S, Royle, JA, Langtimm, CA. 2002. Estimating site occupancy rates when detection probabilities are less than one. ECOLOGY 83:2248-2255.

MacKenzie, DI, Nichols, JD, Hines, JE, Knutson, MG, Franklin, AB. 2003. Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. ECOLOGY 84:2200-2207.

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