Invited Paper

Modeling the Probability of Resource Use: The Effect of, and Dealing with, Detecting a Species Imperfectly

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Abstract

Resource-selection probability functions and occupancy models are powerful methods of identifying areas within a landscape that are highly used by a species. One common design/analysis method for estimation of a resource-selection probability function is to classify a sample of units as used or unused and estimate the probability of use as a function of independent variables using, for example, logistic regression. This method requires that resource units are correctly classified as unused (i.e., the species is never undetected in a used unit), or that the probability of misclassification is the same for all units. In this paper, I explore these issues, illustrating how misclassifying units as unused may lead to incorrect conclusions about resource use. I also show how recently developed occupancy models can be utilized within the resource-selection context to improve conclusions by explicitly accounting for detection probability. These models require that multiple surveys be conducted at each of a sample of resource units within a relatively short timeframe, but given the growing evidence from simulation studies and field data, I recommend that such procedures should be incorporated into studies of resource use. (JOURNAL OF WILDLIFE MANAGEMENT 70(2):367–374; 2006)

Key words

absence, detectability, habitat modeling, occupancy models, occurrence, presence, resource selection.

Resource-selection probability functions (RSPFs) constitute a broad range of analytic techniques that could be used in a multitude of different specific applications (e.g., see Manly et al. 2002); from studying patterns in the use of resource units at the species or population level, to studies of the level of use by specific individuals. In this paper, I focus on study designs in which a sample of resource units surveyed for evidence units are used/not used by a target species during the study period (i.e., at the population level: Design I in the terminology of Manly et al. 2002). Evidence of use by the species may consist of physically observing or capturing animals, hearing calls or vocalizations, or detecting other animal signs (e.g., tracks, droppings, or territorial markings). The basic intent of RSPFs in this situation has been to identify what types of resource units are used by a species during a specific time period compared to unused units, with evidence of selection indicated by categories of resource units with higher probabilities of use. I briefly discuss studies in which independent samples of used units are contrasted to available units, but do not consider them in detail because the methods discussed here to account for imperfectly detecting species are not amenable to the data collected from such designs (although note resulting inferences about resource selection may be equally affected in those study types).

In other areas of ecology and wildlife research, different methodologies have been developed with similar intents (MacKenzie et al. 2005: chapter 2). For example, in metapopulation and island biogeographic studies, habitat patches or islands may be occupied or unoccupied by the target species with the probability of occupancy ultimately being a function of patch characteristics such as patch size or distance from neighboring patches. As such, RSPFs (in the context of Design I studies) can be considered as 1 approach to the general problem of describing or modeling how the presence or absence of a species at a sampling unit (or in the present context, whether a resource unit is used/unused) may depend on characteristics of the sampling unit. Here, I refer to this general class of methods as occupancy models.

In all situations in which occupancy models might be applied, it is important that sampling units (hereafter referred to as resource units) that have been surveyed for the species are correctly classified as used (species present) or not used (species absent), or at worst, the probability of misclassifying a resource unit is equal for all surveyed units. In the latter case, any analysis now provides a relative, rather than an absolute, measure of use (i.e., the ratios of the estimated levels of use between different categories of resource units will be correct, but the actual estimates will be biased). Generally, a resource unit will only be incorrectly classified as used through a data recording/transcription error, or by misidentifying another species as the one of interest. In many situations, it will be possible to largely control for these types of errors with sound data-handling procedures and using well-trained field crews. Similar circumstances could also result in a unit being misclassified as unused, but a more difficult to control source of error is the imperfect detection of a species.

In many situations, it seems reasonable to expect that the target species will not always be detected within a unit that is currently being used, particularly for cryptic or low-density species. For example, in a timed audio or visual encounter survey, the species may simply fail to call or move within your field of view during the timed period, or be temporally absent from the resource unit (e.g., in another part of its home range). When looking for tracks or other animal signs as evidence that a unit is used, the species may be undetected because surveys were randomly located at locations within a unit where there was no recent animal sign even though the unit as a whole was used by the species, or the observer simply missed the animal sign during the search. Nor does modern technology fully resolve the detectability issue. It is well known that individuals fitted with radiotracking or Global Positioning System (GPS) collars may not always be located due to factors such as terrain, canopy cover, or number of available satellites

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(Frair et al. 2004 and references therein). If use of a resource unit by the species is determined by locating individuals fitted with such devices, a unit may be recorded as *unused* even though the individual was within the resource unit, but researchers were unable to obtain a fix on the animal's present location.

There is a growing literature from the analysis of empirical data that would suggest imperfectly detecting the target species is a common problem in many wildlife studies (e.g., MacKenzie et al. 2003, Bailey et al. 2004, Olson et al. 2005, Wintle et al. 2005). Without explicitly accounting for detectability, any modeling of the data is simply a representation of the observers' ability to find the species in the resource units (a combination of true use and the employed sampling methods), not necessarily which resources units are being used by the species. This problem is common to all resource-selection studies. In this paper, I give an example in which resource units are surveyed and classified as used/unused to illustrate how not accounting for detectability may result in misleading conclusions about resource selection. I also discuss the findings of other authors who have explored the same issue in similar contexts. Finally, I discuss a potential solution using recently developed occupancy models that explicitly account for imperfect detection and indicate the consequences for the collection of field data.

The Effect of Imperfect Detection

As noted above, when the target species is likely to be detected imperfectly, resource units cannot be reliably classified as unused; it may have been used by the species but simply undetected by the employed sampling methods. Therefore from such data, without accounting for the imperfect detection of the species, the level of use for a set of resource units can only be considered as a relative, rather than an absolute, measure. However, even as a relative measure, conclusions about selection probabilities of the species will only be reliable if the probability of detecting the species is equal in all resource units.

For example, suppose a state park could be divided into 1,000 resource units, and resource units could be broadly classified into 3 types based on the dominant habitat within each unit: 1) forested, 2) river or swamp, and 3) open grassland. Respectively, the 3 classifications represent 40%, 20%, and 40% of the total resource units. Suppose the intent of this hypothetical study is to investigate the level of resource selection by the fabled moose *Alces alces mickerii*; commonly known as Mickey Moose. Over the course of the study, Mickey Moose uses 500 of the total resource units, or when broken down by habitat type; 280 of the forested units are used, 100 of the river/swamp units and 120 of the grassland units. The probability of use (w_i^*; following the notation of Manly et al. 2002) is therefore 0.7 (= 280/400), 0.5 (= 100/200) and 0.3 (= 120/400) for habitat types forested, river or swamp, and grassland, respectively. Because the probability of use is highest for forested units and lowest for grassland units, there is clearly some form of selection occurring. Expressed as selection ratios (or forage ratios, w_i) we have: 1.4 [= (280/500)/0.4 = 0.56/0.4] for forested units, 1.0 for river or swamp units, and 0.6 for grassland units; giving the same relative values of selection.

Now suppose that Mickey Moose is detected imperfectly. That is, when a used unit is surveyed, there is some chance that evidence of use will not be found, hence a used unit may be misclassified as unused. Let us consider 3 scenarios: 1) detection probability is equal across all units; 2) detection probability is positively correlated with level of use (e.g., units with higher levels of use have higher detection probabilities); and 3) detection probability is negatively correlated with use (e.g., units with higher levels of use have lower detection probabilities). Next, the expected proportion of resource units that would be correctly classified as used (i.e., the expected proportion of used units where Mickey Moose is detected; denoted as $E[w'_i]$) can be simply calculated for category i units as the true proportion of units within that category that are used, times the probability of detecting evidence of Mickey Moose in a used unit (p_i^*), i.e.,

$$E(w'i) = w_i^* p_i^* \quad (1)$$

These expected values are given in Table 1 along with the selection ratios that would result if some of the used units are misclassified as unused due to imperfect detection. Note that only if detection probability is equal across all resource unit types would selection ratios lead to the correct conclusions about resource use for Mickey Moose. When detection probability is positively correlated with level of use, then selection ratios tend to overstate which type of resource units are selected by Mickey Moose, while the converse occurs when detection probability is negatively correlated with level of use. In fact, in the latter case, the indicated level of selection for the 3 types of units is not even in the correct order.

While not specifically examined in the RSPF context, the effect of imperfection detection has been considered via simulation in the closely related situation of habitat modeling. Tyre et al. (2003) and Gu and Swihart (2004) independently showed that the magnitude of habitat effects on the estimated probability of presence (or use) of a species in a sampling unit (equivalent to w_i^*) could be badly biased due to the imperfect detection of the species. The field and analytic methods used in habitat modeling are very similar to those employed in the types of resource-selection studies being considered here. In both cases, a sample of units defined on the landscape are surveyed for the presence or absence of a target species during a certain timeframe. The results of the surveys can be analyzed using logistic regression in which the binary outcome is regressed against variables that are measured on the landscape units (e.g., habitat type). Hence, the conclusions of Tyre et al. (2003) and Gu and Swihart (2004) are equally applicable to the resource selection context.

From the above simple example and the work of Tyre et al. (2003) and Gu and Swihart (2004), it is clear that detection probability has the potential for resulting in misleading conclusions about resource selection, and without the power of omniscience, the issue at hand is how to determine whether detection probability may be having an undue influence on apparent results. I suggest that the key is to collect the necessary data and use methods of analysis that explicitly incorporate detection probability.

Dealing with the Imperfect Detection of a Species

There are 4 general ways in which detection probability could be dealt with: 1) assume it is a nonissue, 2) assume a fixed value(s), 3) use an estimated value(s) from a similar study on the same species, and 4) collect appropriate data within the current study such that

Table 1. Effect of detection probability (p^*) on the expected proportion of resource units correctly classified as used by the fictitious Mickey Moose [$E(w_i)$] and apparent selection ratios ($\hat{w}_i$) for resource units categorized as forested, river/swamp or grassland, under 3 different scenarios: 1) detection probability is equal across all units; 2) detection probability is positively correlated with level of use; and 3) detection probability is negatively correlated with use. Included is the true proportion of used units (w_i^*) and selection ratios (w_i).

	Forested	River/Swamp	Grassland	Overall
w_i^*	0.7	0.5	0.3	0.5
w_i	1.4	1.0	0.6	
		Scenario 1		
p^*	0.8	0.8	0.8	
$E(w_i')$	0.56	0.40	0.24	0.40
$\hat{w}_i$	1.4	1.0	0.6	
		Scenario 2		
p^*	0.9	0.8	0.5	
$E(w_i')$	0.630	0.400	0.150	0.392
$\hat{w}_i$	1.607	1.020	0.383	
		Scenario 3		
p^*	0.5	0.8	0.9	
$E(w_i')$	0.350	0.400	0.270	0.328
$\hat{w}_i$	1.067	1.220	0.823	

detection probabilities relevant to the study can be incorporated explicitly within the analysis.

As illustrated above, imperfectly detecting a species can result in misleading conclusions about resource selection. Whether it is a nonissue in any particular situation depends on the assumptions that the probability of detection is near 1 or that it is constant across the landscape; assumptions that are often difficult to justify objectively. Assuming fixed or estimated values for detection probabilities from other studies (such as from a sightability model; e.g., White and Shenk 2001) may not lead to more reliable inference about resource use if the values are not appropriate for the data and population of interest. Discrepancies may arise because the population from which the detection data was collected was subtly different, due to slight differences in the surveying techniques (e.g., different field methods, different field crews, etc.), or simply as a result of sampling the same population for resource use at a different point in time.

A more robust approach is to design a study such that appropriate data are collected that will provide estimates of detection probabilities specific to the present study. That is, collect appropriate data that will enable the simultaneous construction of a species sightability model and a corresponding RSPF. One approach for doing so that has been used successfully in other contexts is to conduct multiple surveys of each sampling or resource unit within a relatively short timeframe. The multiple surveys of units in which the species was detected at least once supplies information on detection probabilities that can then be applied to those units where the species is never detected to correct the RSPF for false absences (units where the species was present but never detected; Geissler and Fuller 1987, Azuma et al. 1990, MacKenzie et al. 2002, Nichols and Karanth 2002, Tyre et al. 2003, Stauffer et al. 2004). Key to such an approach is the length of time during which the multiple surveys are conducted (referred to as a sampling season by MacKenzie et al. 2005), which should be carefully selected given the objectives of the study and biology of the target species (MacKenzie 2005, MacKenzie and Royle 2005; see the Discussion section for further details).

Statistical Methods

Given that each resource unit has been surveyed for the species multiple times, one approach would be to simply assume that if the species was detected there at least once then the unit is used, and nondetection equates to the unit being unused. Standard logistic regression could then be applied to the used/unused data. However, even after multiple surveys, the species may still be declared falsely absent from resource units resulting in biased estimates of the logistic regression parameters with respect to true use of the resource units by the species (Tyre et al. 2003, Gu and Swihart 2004). A more efficient use of the data is to explicitly estimate detection probabilities while studying the level of resource selection. While not developed within the resource-selection context, a number of independent methods have been developed in other areas of ecology and wildlife management that could easily be applied here (Geissler and Fuller 1987, Azuma et al. 1990, MacKenzie et al. 2002, Nichols and Karanth 2002, Tyre et al. 2003, Stauffer et al. 2004). The most flexible of these modeling procedures is that developed by MacKenzie et al. (2002), of which a brief overview is provided below (see also MacKenzie et al. 2004, 2005 for further details). The basic model consists of 2 components; the first component models the occurrence or presence–absence of the species (which could be regarded as a RSPF in this context); and the second component models whether the species is detected or not in the multiple surveys. Modeling the 2 components simultaneously from appropriately collected data ensures the estimated detection probabilities are relevant to the population of interest, and also that parameter estimates have the correct variance–covariance structure.

The general modeling procedure of MacKenzie et al. (2002) is straightforward. For each unit consider the sequence of detections (1) and nondetections (0) that resulted from the multiple surveys (a detection history). Assuming that the units were either always used or always not used by the species during the sampling season, develop a verbal description of the stochastic processes that may have resulted in each observed detection history. Using defined model parameters to represent the stochastic processes, the probability of observing a particular detection history can be obtained by translating the verbal description into a mathematical equation. The probability statements for each of the resource units can then be combined to form a model likelihood, which can in turn be used to estimate the parameters using any likelihood-based estimation procedure (e.g., maximum-likelihood theory or Bayesian approaches).

For example, let w_i^* be the probability that the ith resource unit is used by the species (notated as ψ_i in the above references, but changed here for consistency with Manly et al. 2002) and p_{ij} be the probability of detecting the species in the jth survey of unit i, given the unit is used. Note that i is now being used to index the individual resource units rather than just the different categories of resource units as above and in Manly et al. (2002). Also note that these parameters cannot be estimated separately for each resource unit, and that they can only vary according to some functional relationship with variables measured at each unit (e.g., via the

logistic equation), or by imposing a distributional assumption upon them (e.g., beta or logit-normal). Suppose that at unit 1, 3 surveys are conducted with the resulting detection history being {010}. A verbal description of this history would be: the species used the unit (as it was detected at least once), not detected in survey 1, detected in survey 2, and not detected in survey 3. Translating this into a mathematical equation to represent the probability of observing this sequence gives $w_1^*(1 - p_{11})\, p_{12}(1 - p_{13})$. Now suppose that at a second resource unit, the species was never detected during the 3 surveys; i.e., the detection history {000} was observed. Here, the verbal description would be: the species used the unit but was never detected, or the species was not using the unit during the surveying period. The corresponding mathematical translation is $w_2^*(1 - p_{21})(1 - p_{22})(1 - p_{23}) + (1 - w_2^*)$, where the first term represents the probability of a false absence, or misclassifying the unit as unused by never detecting the species, [i.e., $w_2^*(1 - p_{21})(1 - p_{22})(1 - p_{23})$] and the second term is the probability that the unit is genuinely unused by the species [i.e., $(1 - w_2^*)$]. The addition of the 2 terms represents that both explanations are possible for the observed data, as denoted by the or statement in the verbal description.

MacKenzie et al. (2002) noted than an important assumption of their model was that the species was either always present or always absent from the resource units for the duration of the repeated surveys. This assumption can be relaxed, however, and parameter estimates are still valid if the physical presence of the species within a resource unit at the time of a survey can be regarded as completely random, although one's interpretation of the parameters must change (MacKenzie 2005). In the former situation, the parameter w_i^* relates to where the species is during the sampling period, while in the latter it relates to where the species is sometimes during the sampling period, which is consistent with how use is often defined in resource studies (L. L. McDonald, Western Ecosystems, personal communication).

As mentioned above, the use and detection probabilities may be functions of variables measured at the resource unit ($x_1, \ldots, x_r$). While there is a range of functions that could be used, the logistic equation (or logit link) is discussed here because of the direct comparison with logistic regression. Because resource units are assumed to be used/not used for the duration of the surveying, then the x variables are also expected to be constant over the same period (Eq. 2). Detection probabilities may be affected by the same type of variables (e.g., habitat type may affect both the level of use by the species, and the observers' ability to find the species within a used unit), but also by variables that may be specific to each survey occasion ($z_1, \ldots, z_s$; e.g., local weather conditions; Eq. 3)

$$w_i^* = \frac{\exp(\beta_0 + \beta_1 x_{1,i} + \ldots + \beta_r x_{r,i})}{1 = \exp(\beta_0 + \beta_1 x_{1,i} + \ldots + \beta_r x_{r,i})} \tag{2}$$

$$p_{ij} = \frac{\exp(\theta_0 + \theta_1 x_{1,i} + \ldots + \theta_r x_{r,i} + \theta_{r+1} z_{1,i,j} + \ldots + \theta_{r+s} z_{s,i,j})}{1 + \exp(\theta_0 + \theta_1 x_{1,i} + \ldots + \theta_r x_{r,i} + \theta_{r+1} z_{1,i,j} + \ldots + \theta_{r+s} z_{s,i,j})} \tag{3}$$

As such, the modeling approach of MacKenzie et al. (2002) can be considered as a logistic regression-based RSPF, automatically corrected with a second logistic regression-based detectability or sightability model for the species.

Examples

Mickey Moose

Consider once again the fictitious Mickey Moose example given above. Suppose that rather than resource use being determined from only a single survey with the detection probabilities given in Table 1, p^* actually represents the probability of detecting the species at least once from 2 independent surveys of the resource units (e.g., from 2 separate visits to the units; 2 observers surveying independently within each unit; or 2 randomly located transects within each unit). Therefore, p^* can be expressed as a function of the probability of detecting Mickey Moose in a single survey of a used resource unit; i.e., $p^* = 1 - (1 - p)^2$ (assuming p is equal in the 2 surveys). Based on this information, for the scenarios considered in Table 1 it is possible to calculate the expected number of resource units where the species would be detected in both surveys, only the first survey, only the second survey, or never detected (i.e., the expected number of units with the detection histories 11, 10, 01, or 00, respectively). For each habitat type, use and detection probabilities can be allowed to differ simply with a series of dummy variables that indicate the classification of each resource unit. Applying the modeling approach of MacKenzie et al. (2002), resulting estimates are unbiased with the probability of use correctly estimated as 0.7 for forested units, 0.5 for rivers and swamps, and 0.3 for grasslands, regardless of how detection probability varied between unit types.

Pronghorn Antelope

Manly et al. (2002) use data collected on pronghorn antelope (*Antilocapra americana*) at 256 locations in Wyoming, USA, over 2 consecutive winters 1980–1981 and 1981–1982 (Ryder 1983) as an example of applying resource-selection functions. They note that in this instance use could be defined in a number of ways (Manly et al. 2002:90), and clearly, estimates of the probability of use varies with the definition. For the sake of illustration, here it is assumed that use of the resource units is the same in both winters (i.e., if a unit is used in 1 winter, it is also used in the other), hence, the 2 winter surveys could be regarded as repeated surveys of the units. Therefore, if pronghorn antelope were detected at a resource unit in at least 1 of the winters, the location is regarded as used. Some readers may (rightly) question the reasonableness of assuming a consistent pattern of resource unit use for pronghorn antelope in both winters. There may be a number of factors that would cause resource use to be different in different winters, in which case inferences from the below analyses may be unreliable with respect to the true situation for pronghorn antelope. However, the analyses do serve to illustrate how results may be misleading for similar data collected from situations in which the assumption of consistent use during the period of repeated surveying is reasonable.

As mentioned above, ignoring detection probability, one approach would be to assume that if pronghorn antelope were not detected in either winter a unit is unused and analyze the data with logistic regression. However, at only 30% of the units in which pronghorn antelope were detected in at least 1 winter, were they detected in both, indicating that pronghorn antelope were

not detected perfectly in used units. Hence, there is a possibility that some of the resource units in which pronghorn antelope were not sighted in either winter were actually being used. Note that in this instance, pronghorn antelope may not be detected in a used resource unit simply due to the observers missing any physical evidence of them, or due to pronghorn antelope being temporally absent from the unit at the time of the survey. Without accounting for this potential misclassification of used units, results could be misleading as techniques such as simple logistic regression only models in which antelope were sighted during the 2 winters; a combination of true use and detectability.

To illustrate this, here I conducted 2 analyses. The first uses simple logistic regression where a unit was assumed to be unused by pronghorn antelope if they were never sighted within the unit in either of the 2 winters, and used otherwise. The second uses the method of MacKenzie et al. (2002), which simultaneously models both use and detectability. Units were coded with detection history {00} if antelope were not detected in either year, {10} if antelope were detected the first winter and not the second, and so forth. In both analyses, a set of variables that may potentially affect the probability of use of a resource unit (and also the probability of detecting pronghorn antelope within a used unit) were considered. In the interests of brevity, only a subset of the variables presented in Manly et al. (2002) were utilized here, and no comparison with their results are made because of the different manner in which use is defined. The variables considered here were sagebrush density (bushes/ha; *Sg*), slope (%; *Sl*), distance to water (kms; *DW*) and aspect (*A*). Akaike's Information Criterion (AIC) is used to rank the set of considered models in order of parsimony: models that capture the main aspects of the data with a minimal number of parameters (models with lower AIC values are considered to be more parsimonious). Model weights (Burnham and Anderson 2002) were also calculated from the AIC values to indicate the level of support for each model considered. In addition, to get an overall indication of how important particular variables may be with respect to the RSPF, model weights were summed for all models with that particular variable (Burnham and Anderson 2002). Variables with high summed model weights could be considered as more important in terms of explaining variation in the response or dependent variable. Also note that both analyses assume resource-unit use is consistent due to the manner in which use has been defined here.

Using the simple logistic regression approach, distance from a water source and slope were found to be the most important variables for determining use (Table 2). The summed model weights for these variables were 90% and 55%, respectively, while the summed model weights for the remaining variables were 38% (sagebrush density) and 19% (aspect). The logistic regression coefficients for the water source and slope variables from the highest-ranked model were both negative suggesting that the probability of a resource unit being used was lower for units that are further away from water sources and have greater slopes.

Somewhat different conclusions were obtained when the modeling approach of MacKenzie et al. (2002) was used to construct a RSPF. Maintaining a general model for the detectability component, distance from a water source no longer appeared to be very important in terms of resource selection (Table 3). Models where use was a function of distance from a water source now comprised only 29% of the model weights. Slope (55%) and sagebrush density (41%) appear to be the most important variables for determining the use of resource units, with aspect ranking as least important (6%). In this situation, none of the variables appeared to be overwhelmingly important with the constant use model ($w^*(\cdot)$) being ranked second and having 16% of the model weights. From the top-ranked model, probability of use decreased as slope increases.

Table 2. Summary of model-selection procedure examining factors affecting the probability of apparent use (w') of resource units by pronghorn antelope during the winters of 1980–1981 and 1981–1982 using simple logistic regression. Factors considered are sagebrush density (*Sg*), slope (*Sl*), distance to water (*DW*) and aspect (*A*). The model with equal probability of apparent use for all resource units is denoted as $w'(\cdot)$. Reported is twice the negative log-likelihood (–2*l*), the number of parameters in the model (*K*), the relative difference in AIC values compared to the top-ranked model (ΔAIC), and the AIC model weights (*W*).

Model	–2*l*	*K*	ΔAIC	*W*
$w'(Sl + DW)$	345.26	3	0.00	23%
$w'(DW)$	347.48	2	0.22	21%
$w'(Sg + Sl + DW)$	344.08	4	0.82	16%
$w'(Sg + DW)$	346.44	3	1.18	13%
$w'(Sl + DW + A)$	342.05	6	2.79	6%
$w'(DW + A)$	344.34	5	3.08	5%
$w'(Sl)$	351.07	2	3.81	3%
$w'(Sg + Sl + DW + A)$	341.31	7	4.05	3%
$w'(Sg + DW + A)$	343.71	6	4.45	3%
$w'(Sg + Sl)$	349.93	3	4.67	2%
$w'(\cdot)$	354.89	1	5.63	1%
$w'(Sl + A)$	347.37	5	6.11	1%
$w'(Sg)$	353.91	2	6.65	1%
$w'(Sg + Sl + A)$	346.71	6	7.45	1%
$w'(A)$	350.93	4	7.67	1%
$w'(Sg + A)$	350.39	5	9.13	0%

Table 3. Summary of model-selection procedure examining factors affecting the probability of use (w^*) of resource units by pronghorn antelope during the winters of 1980–1981 and 1981–1982 using the occupancy model of MacKenzie et al. (2002), with a general model for detection probabilities (i.e., $w(Sg + Sl + DW + A)$). Factors considered are sagebrush density (*Sg*), slope (*Sl*), distance to water (*DW*), and aspect (*A*). The model with equal probability of apparent use for all resource units is denoted as $w^*(\cdot)$. Reported is twice the negative log-likelihood (–2*l*), the number of parameters in the model (*K*), the relative difference in AIC values compared to the top-ranked model (ΔAIC), and the AIC model weights (*W*).

Model	–2*l*	*K*	ΔAIC	*W*
$w^*(Sl)$	615.48	9	0.00	23%
$w^*(\cdot)$	618.20	8	0.72	16%
$w^*(Sg + Sl)$	614.33	10	0.85	15%
$w^*(Sg)$	616.60	9	1.12	13%
$w^*(Sl + DW)$	615.44	10	1.95	9%
$w^*(DW)$	617.73	9	2.25	7%
$w^*(Sg + Sl + DW)$	614.33	11	2.85	6%
$w^*(Sg + DW)>$	616.47	10	2.99	5%
$w^*(Sl + A)$	615.01	12	5.53	1%
$w^*(A)$	617.53	11	6.05	1%
$w^*(Sg + Sl + A)$	613.89	13	6.41	1%
$w^*(DW + A)$	616.08	12	6.60	1%
$w^*(Sl + DW + A)$	614.35	13	6.87	1%
$w^*(Sg + A)$	616.51	12	7.03	1%
$w^*(Sg + Sl + DW + A)$	613.69	14	8.21	0%
$w^*(Sg + DW + A)$	615.83	13	8.34	0%

Note that rather than maintaining a general model for detection probability, an alternative approach would have been to find a parsimonious model (or a small set of models) for detection probability prior to performing model selection with respect to resource use. The purpose of this may be to reduce the number of parameters being estimated and, in some applications, the factors that affect detectability or sightability of the species may also be of interest. Provided that the parsimonious model captures the main features of the data in a similar manner to the full or general model (which is one of the purposes of using a model-selection procedure) then similar results should be obtained. The results of using this approach are not presented here, but note that resulting inferences about resource selection by pronghorn antelope were relatively unchanged. Interestingly, in this case, the most parsimonious model was found to be one in which detection probability was only a function of distance to a water source. This suggests that when using the simple logistic regression approach, the reason distance to water appeared important may have been due to pronghorn antelope being sighted more readily closer to water (possibly due to them congregated near drinking water) rather than them actually using a greater fraction of units near water compared to other units in the landscape. Furthermore, there was comparatively little support for the model where detection probability was constant for all resource units with only 6% of the AIC model weight. This constant detectability model is equivalent to the implicit assumption required to interpret the results of logistic regression as a valid relative measure of resource use, and performing model selection on the RSPF component while maintaining this constant p model provided very similar results to simple logistic regression. This corroborates my earlier claim that when not adequately accounting for detection probability, any modeling procedure only describes a combination of the unit being used and the animals being detected there.

Discussion

Here, I have demonstrated that when species are detected imperfectly, then misleading conclusions about how the species selects and uses resource units may result. While in the Mickey Moose example, detection probability was correlated with habitat use, the 2 quantities do not have to be correlated for misleading inferences to result, only that detection probabilities may be different for different categories of resource units. This can be especially problematic when factors that might be considered as predictor variables for resource selection, could also influence detection probability, as in the pronghorn antelope example. This influence of detection probability on resulting inferences about resource selection is unlikely to come as an epiphany for most readers, however, the purpose of this article is to bring to the reader's attention that analytic methods have been developed in other areas of ecology and wildlife management that explicitly account for detection probability that may be usefully applied in the resource selection context.

These recently developed occupancy models require resource units to be surveyed multiple times within a sampling season to estimate detection probability. It is important to note that the requirement of multiple surveys does not necessarily translate to requiring that each resource unit must be visited on a number of discrete occasions. There are a number of practical options to how the multiple surveys may be conducted, for example using multiple independent observers, or surveying multiple plots within a larger resource unit. How the multiple surveys are conducted in practice deserves very careful attention as it can subtly alter how *use* is to be interpreted. Similarly, as mentioned above, the length of the season should also be carefully considered with respect to the objective of the study and biology of the species. As the intent of the study is often to provide a snapshot of the resource selection of the species at a certain point in time, the length of the season should be minimal in some sense, otherwise there is potential for changes to occur within the system; blurring understanding about resource selection. If the sampling season is too long, then a species may appear to use all resource units within the study area, while too short a season may provide insufficient opportunity for researchers to encounter the target species in some categories of resource units. While not specifically in the RSPF context, readers are directed to MacKenzie (2005), MacKenzie and Royle (2005), and MacKenzie et al. (2005) for details of these and other design considerations.

I also want to stress the general study protocol that has been assumed here. An area is identified (comprised of a large number of resource units) where managers or researchers wish to learn about the resource selection, or more generally the occurrence, of a target species. This area is the statistical population of interest and defines the scope of inference for any analysis of data subsequently collected from it. In the language of resource selection, this identified area determines the resource units available to the species. A probabilistic sampling scheme (e.g., random) is used to then select units from this population that are repeatedly surveyed for the species with the species being detected or not detected in each survey, and data that may be used to characterize a resource unit (e.g., habitat type) is also collected. Used and unused units are not sampled independently; there is a single sample of available units and use is determined through the repeated surveys. I would suggest that inferences from studies in which a sample of available units is compared to a sample of used or unused units may be inaccurate due to the imperfect detection of the species (i.e., resource units that are known to be used may represent a nonrandom subset of units that are truly used by the species).

It is also fundamental to realize that how one defines which units are available to the species (i.e., how one defines the population of resource units of interest) may influence the resulting inferences about resource selection. Even though information from a census or independent sample of available units is not used directly within the estimation procedure outlined here (unlike with a selection ratio, for example), different definitions may subtly alter the true RSPF that we are attempting to estimate simply because the single sample is collected for a different available collection of resource units. I stress that in any study, one should always clearly define the population of sampling units that is of interest prior to data collection, and select units from that population using a probabilistic sampling scheme (e.g., simple random sampling). Inferences from any data analysis are always conditional upon the sampling methods used, and generalizing results to different populations (e.g., by defining availability differently) may not be appropriate.

Similarly, how one should interpret *use* depends very much on the exact field and sampling methods that have been employed, regardless of the analytic methods applied to the resulting data. Once again, it must be realized that the conclusions one draws from a statistical analysis is inextricably linked to how that data was collected from the field. Different sampling methods may indicate different patterns of resource use even for the same population. Ideally, one should begin with a clear sense of how they wish to interpret use, then implement sampling and field protocols (and apply appropriate analytic methods) to achieve that end.

Here, I have only considered situations in which the desire is to construct a RSPF at the species level (i.e., a Design I study type). When interest is at the individual level, it is likely that the imperfect detection of individuals may again result in misleading conclusions about resource use, even when individuals are fitted with a radiotransmitter or GPS device (Frair et al. 2004). Further research is needed to assess the potential impact of imperfectly detecting individual animals in resource-selection and utilization functions, and analytic methods that account for detection probabilities may have to be developed.

How resource selection (at the population level) changes over time, and the factors that may drive such changes, may also be of interest in some applications. Similar to above, misleading conclusions may result if detection probability is different at different points in time. The extension of the above methods by MacKenzie et al. (2003; see also MacKenzie et al. 2005) to modeling the occurrence of a target species across a landscape at multiple points in time, accounting for detecting the species imperfectly, may be useful. It would be possible to estimate the probability that a resource unit used at the previous point in time became unused, and the factors that may affect that probability (i.e., changes in habitat in the intervening period or changes in generalized weather patterns). MacKenzie et al. (2003) referred to this process as a local extinction of the species. The other process they refer to is colonization. In the resource selection context, this is when a previously unused unit becomes used between 2 points in time. Again, to be able to estimate and accommodate for the imperfect detection of the species then repeat surveys are required at each point in time.

Finally, the occupancy models discussed above have been incorporated into Windows-based software: program PRESENCE, which was specifically developed for modeling occupancy-type data and is freely available for download from http://www.proteus.co.nz; and some techniques have been incorporated into program MARK (http://www.cnr.colostate.edu/~gwhite/mark/mark.htm), which was originally developed for the application of capture–recapture models to data collected on marked individuals.

Management Implications

RSPFs may be used to identify highly utilized habitats in a landscape that subsequently could be protected for the successful ongoing management or conservation of a species. However, as demonstrated above, imperfectly detecting a species may lead to erroneous conclusions about resource use, and hence inappropriate management decisions, if not suitably accounted for within a statistical analysis. As issues of species detectability can not be ignored, the main implication in advocating the use of the above occupancy models is to argue that monitoring and data collection programs must be carefully designed to provide quality data of a type amenable to such analytic techniques, given management objectives (see MacKenzie et al. 2005: Chapter 6, and references therein). Primarily: 1) auxiliary information is required to estimate detection probability (e.g., repeated surveys), thus enabling separation of false and true absences; 2) factors that may affect detection probability also need to be considered to avoid introducing heterogeneity that may bias estimates of resource use; and 3) the overall program design and manner of selecting resource units to survey must enable an assessment of the specific management objectives. By collecting appropriate data, management will be able to make more reliable inferences about resource use through the application of occupancy models.

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