Research Article

Estimating Site Occupancy and Detection Probability Parameters for Meso- And Large Mammals in a Coastal Ecosystem

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Abstract

Large-scale, multispecies monitoring programs are widely used to assess changes in wildlife populations but they often assume constant detectability when documenting species occurrence. This assumption is rarely met in practice because animal populations vary across time and space. As a result, detectability of a species can be influenced by a number of physical, biological, or anthropogenic factors (e.g., weather, seasonality, topography, biological rhythms, sampling methods). To evaluate some of these influences, we estimated site occupancy rates using species-specific detection probabilities for meso- and large terrestrial mammal species on Cape Cod, Massachusetts, USA. We used model selection to assess the influence of different sampling methods and major environmental factors on our ability to detect individual species. Remote cameras detected the most species (9), followed by cubby boxes (7) and hair traps (4) over a 13-month period. Estimated site occupancy rates were similar among sampling methods for most species when detection probabilities exceeded 0.15, but we question estimates obtained from methods with detection probabilities between 0.05 and 0.15, and we consider methods with lower probabilities unacceptable for occupancy estimation and inference. Estimated detection probabilities can be used to accommodate variation in sampling methods, which allows for comparison of monitoring programs using different protocols. Vegetation and seasonality produced species-specific differences in detectability and occupancy, but differences were not consistent within or among species, which suggests that our results should be considered in the context of local habitat features and life history traits for the target species. We believe that site occupancy is a useful state variable and suggest that monitoring programs for mammals using occupancy data consider detectability prior to making inferences about species distributions or population change. (JOURNAL OF WILDLIFE MANAGEMENT 70(6):1625–1633; 2006)

Key words

Cape Cod, detection probability, mammals, monitoring, multispecies, nondetection, presence-absence, site occupancy.

Documentation and monitoring of biological diversity will be a leading conservation challenge in the 21st century (Wilson 1992). To meet that challenge, a number of large-scale monitoring programs have been established to document and track specific taxonomic groups (e.g., North American Breeding Bird Survey, Amphibian Research and Monitoring Initiative). However, monitoring programs often focus on species that are considered ecological indicators or that generate public interest (e.g., amphibians exhibiting malformations, neotropical migrant birds) (Noss 1990, Niemi et al. 1997). With the exception of charismatic megafauna and game species, relatively little attention has focused on mammals (but see Newman et al. 2003). The vast majority of mammal species are nocturnal, cryptic, and elusive, which makes them difficult to inventory or monitor (Hoffmann 1996). As a group, mammals are characterized by broad differences in body size, morphology, and life history strategies that often require species-specific sampling methods (Jones et al. 1996). The resulting cost and effort can hinder multispecies monitoring efforts. For example, only 30% ($n = 153$) of U.S. national parks initially selected meso- or large mammals as vital indicators worthy of monitoring (S. Fancy, National Park Service, personal communication). Nevertheless, mammals often play pivotal roles in the functioning of ecosystems: carnivores can influence prey species that, in turn, can have a cascading effect on other system components (Crooks and Soulé 1999); overabundant herbivores like white-tailed deer (*Odocoileus virginianus*) can alter vegetative succession (Alverson et al. 1988); and introduced species like nutria (*Myocastor coypus*) and feral hogs (*Sus scrofa*) can devastate entire ecosystems. Indeed, much remains to be learned about how mammals function in different environments, especially in human-dominated landscapes (Andrén 1994, Crooks 2002).

To gather such information, monitoring programs are needed that can provide unbiased estimates of biological variation and changes that occur over time and space (Boulinier et al. 1998, Yoccoz et al. 2001). Unfortunately,

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many programs fall short of these goals (Thompson et al. 1998). Although a variety of direct and indirect survey methods are available to sample mammals and document their occurrence (e.g., counts of fecal material, scent station surveys, captures, or harvest per unit effort), results are often reported as indices of relative abundance or harvest. For example, much of the scientific information available on furbearers comes from harvest records that are inherently biased as estimates of abundance, and they do not provide reliable monitoring data (Ray 2000). Study plans and sampling routines that generate indices are relatively easy to design and implement, but the relationship between the count and the target population is often unknown and can take many forms (Conroy 1996, Bailey et al. 2004), rendering the index problematic as a representation of the parameter of interest (Anderson 2001). In addition, indices require assumptions that are unlikely to be true in practice (MacKenzie and Kendall 2002). One such assumption is that detectability of a species is stable across time and space. Although methods for estimation of detection probabilities to improve estimates of species presence or site occupancy have received little attention and are relatively new (Geissler and Fuller 1986, MacKenzie et al. 2002, Royle and Nichols 2003), site occupancy provides a reasonable measure for estimation of status and change, and it also provides a credible, cost-effective alternative for large-scale, multi-species monitoring programs when specific individuals cannot be identified (Pollock et al. 2002, Bailey et al. 2004).

Our objectives were to use detection and nondetection data to estimate detection and site occupancy probabilities for terrestrial meso- and large mammals occurring on Cape Cod, Massachusetts, USA, as a precursor to establishing a long-term multispecies monitoring program. We explored whether survey method, vegetation type, or seasonality influenced our ability to detect target species. We used our estimates of detection probability to estimate the sampling effort needed to determine occupancy state (presence-absence) for a target species at a site.

Study Area

We conducted all field work in Cape Cod National Seashore, a unit of the National Park Service that covered about 20% of the Cape Cod peninsula (approx 20,000 ha) in eastern Massachusetts (Fig. 1). Surficial geology of the region consists of glacial deposits characterized by outwash plains and lake deposits (i.e., kettle ponds) and extensive dune systems (Oldale and Barlow 1986). Topography and vegetation communities were typical of north Atlantic barrier islands (Oosting 1954), specifically characterized by pitch pine (*Pinus rigida*)–mixed oak (*Quercus* spp.) forests, heathlands, grasslands, sand dunes, cedar swamps, salt marshes, and intertidal mudflats. Dominant plants included American beachgrass (*Ammophila breviligulata*), Atlantic white cedar (*Chamaecyparis thyoides),* salt marsh cord grass (*Spartina alterniflora*), common reed (*Phragmites australis),* bearberry (*Arctostaphylos uva-ursi*), shadbush (*Amelanchier canadensis*), pitch pine, red oak (*Quercus rubra*), black oak (*Quercus velutina*), scrub oak (*Quercus ilicifolia*), and black cherry (*Prunus serotina*). Climate was characterized by cold winters and rainy, warm summers (Fletcher 1993). A variety of historic land uses and disturbances that include agriculture, hurricanes, human recreation, suburban development, and fire created a landscape mosaic (Patterson et al. 1983, Motzkin et al. 2002), typical of the Atlantic coastal environment.

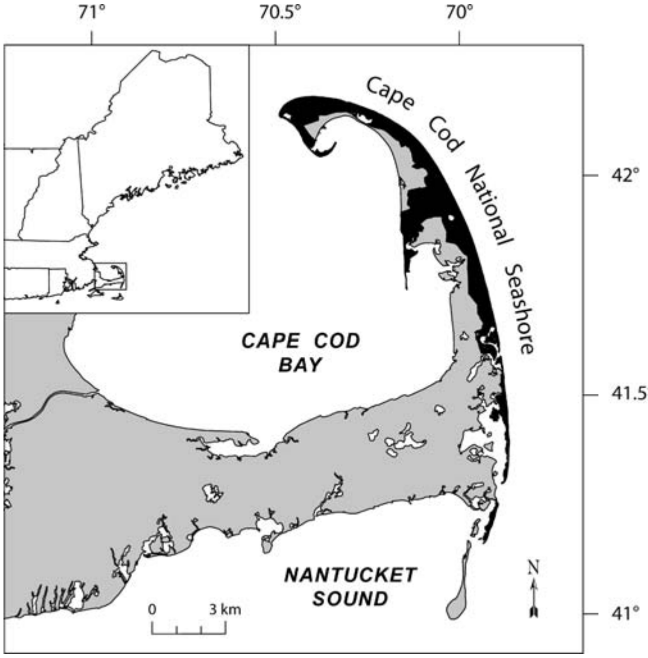

Figure 1. Location of study area (Cape Cod National Seashore) for detecting meso- and large mammals on Cape Cod, Massachusetts, USA, 2001–2002.

Methods

Sampling and Field Methods

We selected sampling sites using a systematic random design stratified by vegetation type to ensure that all 5 major vegetation types found on Cape Cod were represented (i.e., grasslands, heathlands, pine forest, oak forest, and freshwater wetlands). We followed sampling guidelines devised specifically for national parks (see Geissler and McDonald 2003 for details) and selected sites using the program Sample, an Arcview 3.2 extension (Quantitative Decisions, Merion Station, Pennsylvania). We placed a grid of random origin over digital maps of vegetation communities, and to ensure an equal number of points (3) within each of the major vegetation types, we varied the grid cell size (650–1250 m), depending on the extent and configuration of these communities. We generated points by randomly selecting a grid cell and then randomly assigning a single point inside each selected cell. We considered the random points to be the sampling sites for our study, whereas we used the grids as a way to allocate samples among the vegetation types. This design enabled a thorough distribution of points throughout the Seashore and at the same time separated sampling sites to maintain independence. All sampling sites were separated by a distance of >1 km to promote independence, with the exception of 2 groups of points that were 460 m and 650 m apart because they were constrained by vegetation patterns. In one instance we detected the same species at a pair of the closer-spaced sites during a single sampling period, and we used physical evidence collected from detection methods (see below) to determine that the same individual was not detected at both sites. Thus, we assumed independence of our sites with respect to visits by individual animals.

We tested the efficacy of 3 detection methods to detect mammals: remote cameras with infrared sensors (Trailmaster®, Goodson and Associates, Inc., Lenexa, Kansas), hair traps (Baker 1980), and cubby boxes (i.e., covered track plates; Barrett et al. 1983, Zielinski and Kucera 1995, Loukmas et al. 2003). At each sampling site, we constructed detection arrays that consisted of one remote camera and an infrared sensor, 2 hair traps, and 2 cubby boxes. We set devices in a circular fashion with track plates and hair catchers surrounding the camera setup at a distance of 50 m. We provided bait and a generic scent lure at each device. We deployed detection arrays during all seasons of the year, but due to logistics and equipment considerations we did not sample all sites simultaneously. We sampled sites from October 2001 to November 2002, with sampling occasions defined as 1-week intervals for which target species were either detected or not detected by each method. We placed 2–3 arrays in each of the 5 vegetative strata and collected detection and nondetection information at 13 locations. We report occurrences as the number of times a species was detected during a sampling occasion. We developed photographs and visually inspected each print to make identifications. We collected contact sheets from cubby boxes from the field and we conducted species identifications in the lab. We took length and width measurements using calipers to distinguish mustelid species and, in some cases, canid species. We collected hair samples from hair traps using metal forceps and we placed the hair samples in individually labeled plastic vials. We identified hairs to species by comparison of gross morphological features with a reference collection, analysis of hair scale pattern, and medullary characteristics (Stains 1958, Adorjan and Kolenosky 1969, Wallis 1993).

Data Analyses

We classified week-long sampling intervals (occasions) a priori into 4 seasons: Fall 2001 (mid Oct to early Nov), Winter (late Nov to Mar), Spring (Apr to mid Jun), and Fall 2002 (mid Aug to early Nov). Initially, we calculated the number of total detections for each day that a method was operable in the field. This provided a simple measure of efficiency for each sampling method with respect to the number of detections for the target species. Using the method described by MacKenzie et al. (2002), we estimated site occupancy, ψ, and detection probability, p, for all the mammal species that we detected. For this approach there were 3 possible outcomes: 1) the site was occupied and the species was detected, $\psi \times p$; 2) the species was present but not detected, $\psi \times (1 - p)$; and 3) the species was not present and therefore was not detected, $1 - \psi$. We estimated detection probabilities by sampling each site on multiple occasions. The probability was a projected parameter in a maximum likelihood-estimation of the proportion of sites occupied (ψ) during the sample period. We verified that occupancy was closed (i.e., did not change) for all species using the Robust-design models of MacKenzie et al. (2003). This exercise indicated that the occupancy status for each species was constant throughout the study, allowing us to use the closed-occupancy models (MacKenzie et al. 2002) to test the following a priori hypotheses.

In our first analysis, we assumed that detection probabilities and site occupancy were constant across time and space. We used this model to provide a basic description for comparison with the unadjusted (i.e., naïve) proportion of sites where a species was detected, although a constant model of site occupancy and species detectability is not the best representation of the data.

In our second analysis, we considered each species separately and assessed factors that might affect species-specific occupancy or detection probabilities. Our focus was to determine the effectiveness of individual methods for detecting each species, hoping that adjusting for detection probability differences among methods would yield similar species-specific occupancy estimates. This exercise is valuable in 2 ways: 1) it would allow us to evaluate historical studies that did not have the benefit of occupancy estimation methods, and 2) we could assess the appropriateness of making comparisons across studies that differ in their detection method or sampling effort. We constructed a set consisting of 12 candidate models with the following combinations of factors: 1) we modeled species-specific occupancy probability as constant across all sites or as varying according to vegetation type or detection method, and 2) we modeled detection probability as constant across all sampling occasions or varied among seasons, vegetation type, or detection methods. We also considered 2 additional models with detection probabilities modeled as an interactive effect of method × season, whereas occupancy was either constant or varied by detection method. Data limitations prohibited us from considering models with the method × season interaction of detection and vegetation-specific occupancy probabilities. We used only detection methods that documented the target species in this analysis; if a method did not detect the target species at any of the sites we did not include it in the analysis.

As part of constructing these models, we acknowledged a possible lack of independence among detection methods within each site because a single individual could be detected by more than one method. In occupancy models, the effective sample size is generally assumed to be the number of independent sites (MacKenzie et al. 2005). Under these conditions, setting effective sample size (MacKenzie et al. 2005) equal to the number of sites × the number of methods may be too high, thereby altering inference via model selection. To explore the robustness of inferences based on model selection, we considered how results might change

Table 1. Parameter estimates for occupancy (ψ) and detectability (p) of 10 mammal species using 3 detection methods on 13 sites during 43 possible sampling weeks on Cape Cod, Massachusetts, USA, 2001–2002.[a]

		CAM (T = 128)					**CUB (T = 172)**					**HAIR (T= 187)**				
Species	**ψ(min)**	**ψ(obs)**	**$\hat{\psi}(.)$[b]**	**SE$\hat{\psi}(.)$**	**$\hat{p}(.)$[b]**	**SE $\hat{p}(.)$**	**ψ(obs)**	**$\hat{\psi}(.)$**	**SE$\hat{\psi}(.)$**	**$\hat{p}(.)$**	**SE $\hat{p}(.)$**	**ψ(obs)**	**$\hat{\psi}(.)$**	**SE$\hat{\psi}(.)$**	**$\hat{p}(.)$**	**SE $\hat{p}(.)$**
Coyote	0.92	0.83	0.94	0.12	0.21	0.04						**0.54**[c]	**1.00**	**0.00**	**0.05**	**0.02**
Virginia opossum	0.39	**0.17**	**0.21**	**0.14**	**0.16**	**0.09**	0.31	Na[d]		Na		**0.39**	**0.68**	**0.21**	**0.11**	**0.03**
River otter	0.17	0.17	0.17	0.11	0.40	0.11										
Long-tailed weasel	0.23						0.23	0.29	0.14	0.19	0.08					
Striped skunk	0.46	0.33	0.36	0.15	0.27	0.07	0.39	0.60	0.19	0.13	0.04	0.23	0.47	0.25	0.06	0.03
White-tailed deer	0.25	0.25	0.34	0.17	0.16	0.06										
Gray squirrel	0.39	0.17	Na		Na		0.23	0.38	0.19	0.12	0.04					
Cottontail spp.	0.31	0.31	0.34	0.14	0.41	0.07	0.08	Na		Na						
Raccoon	0.85	0.83	0.90	0.12	0.38	0.05	0.69	0.86	0.12	0.25	0.04	**0.31**	**0.55**	**0.23**	**0.08**	**0.03**
Red fox	0.39	0.25	0.28	0.15	0.20	0.10	0.15	Na		Na						

[a] Abbreviations: CAM, cameras; CUB, cubby box; HAIR, hair trap. T is the number of weeks the detection method was deployed at all sites combined. ψ(min) is the proportion of sites where a species was detected using all methods. ψ(obs) is the proportion of sites where a species was detected for the given detection method but is unadjusted for detection probability (i.e., naïve estimate).

[b] Parameter estimates are based on a model with constant occupancy and detection probabilities $\psi(.)\ p(.)$.

[c] Bold entries indicate instances where ψ(min) was not within the interval: $\hat{\psi}(.) \pm 1$ SE (i.e., poor estimates).

[d] Na: model yielded nonsensical occupancy estimates (1.0) because of low detection probability for the given method, $P < 0.02$.

using an effective sample size equal to the number of sites only (13), the most conservative approach possible under our sampling scheme.

In our third analysis, we considered detection and nondetection information for each sampling method separately and determined whether: 1) detection probabilities varied among time (seasons), species, or a combination (species × season interaction), and 2) occupancy probabilities varied among species. This analysis emulates studies where only one detection method is used, in a multispecies monitoring program, for example. If detection probabilities differed among species, then we would have reason to question naïve site occupancy comparisons across species generated by a specific detection method (Boulinier et al. 1998, Moruzzi et al. 2002). We fit 8 candidate models constructed with 2 levels of occupancy (constant or species specific) and 4 levels of detection probability (constant, species specific, season or time specific, or species × season interaction). Similar to the previous analysis, we included only species that were detected by the target method in this analysis; if a species was not detected at any of the sites by the target method, we did not include that species in the method-specific analysis.

Finally, to illustrate how detection probabilities can be used to design inventory programs, we used model-averaged detection estimates to calculate the 95% probability that a target species would be detected at least once at an occupied site in t weeks of sampling. For comparison, we applied the recommendations developed by MacKenzie and Royle (2005) to determine the optimal number of sampling occasions to confirm site occupancy.

All analyses can be performed with either the program MARK (White and Burnham 1999) or PRESENCE 2.0 (Hines and Mackenzie 2004). In our assessment of occupancy closure and factors that influenced both occupancy and detection, we ranked all models according to Akaike's Information Criterion adjusted for small sample sizes (AIC_c; Akaike 1973, Burnham and Anderson 2002). We reported model weights (w_i) that sum to 1 because they provide an indication of the weight of evidence in favor of a given model being the best approximating model within the considered set (Burnham and Anderson 2002).

Results

Over our 13-month study, we recorded 10 mammal species by detection arrays and confirmed support for the static occupancy model ($w_i = 1.0$). Remote cameras detected 9 species and recorded 0.71 visits per active day, which was higher than cubby boxes (7 species detected, 0.060 visits/active day) or hair traps (4 species detected, 0.029 visits/active day). We detected white-tailed deer and river otters (*Lontra canadensis*) only by remote cameras and long-tailed weasels (*Mustela frenata*) only by cubby boxes (i.e., tracks). We detected the remaining 7 species, the Virginia opossum (*Didelphis virginiana)*, gray squirrel (*Sciurus carolinensis*), cottontail (*Sylvilagus* spp.), and 4 mesocarnivores (coyote [*Canis latrans*], striped skunk [*Mephitis mephitis*], raccoon [*Procyon lotor*], and red fox [*Vulpes vulpes*]), by >1 method.

Applying the simplest model with constant occupancy and detection probability to each of the 10 detected species, we found that remote cameras detected 90% of the mammal species in this system (Table 1). Given that the target species is present, remote cameras are ≥3 times more likely than hair traps to detect coyote, striped skunk, cottontail, raccoon, and red fox. Cameras were also equal or superior to cubby boxes for many of these same species, except for the 2 smaller species, long-tailed weasel and gray squirrel (Table 1). Despite being detected by all 3 methods, site occupancy estimates for opossums varied among methods when using this simple model.

Models suggesting that detection probabilities varied among methods were among the best models for all species except opossums (Table 2). Rankings of detection methods based on these models are identical to the data in Table 1,

Table 2. Selected estimates of occupancy (ψ) and detection (p) probabilities using the best approximating models for 7 mammal species on Cape Cod, Massachusetts, USA, 2001–2002.

Species	Models[a]	w_i[b]	$\hat{p}_{\text{CAM}}$[c,d]	$\hat{p}_{\text{CUB}}$	$\hat{p}_{\text{HAIR}}$	$\hat{\psi}_{\text{CAM}}$	$\hat{\psi}_{\text{CUB}}$	$\hat{\psi}_{\text{HAIR}}$
Coyote	ψ(.) p(method)	0.78	0.20		0.06	0.96		0.96
	ψ(method) p(method)	0.20	0.21		0.05	0.94		1.0
	Model averaged estimates		0.20		0.05	0.94		0.96
	SE		0.04		0.02	0.11		0.09
Opossum	ψ(.) p(season)	0.63				0.62	0.62	0.62
	ψ(veg) p(season)	0.15						
	ψ(method) p(season)	0.10				0.35	0.62	0.82
	Model averaged estimates					0.60	0.63	0.66
	SE					0.18	0.17	0.17
Striped skunk	ψ(.) p(veg)	0.50				0.62	0.62	0.62
	ψ(veg) p(method)	0.16	0.24	0.13	0.06			
	ψ(.) p(method)	0.10	0.26	0.13	0.07	0.46	0.46	0.46
	Model averaged estimates		0.21	0.13	0.08	0.60	0.60	0.58
	SE		0.08	0.03	0.04	0.17	0.17	0.17
Raccoon	ψ(.) p(method)	0.49	0.38	0.25	0.05	0.85	0.85	0.85
	ψ(veg) p(method)	0.33	0.39	0.25	0.06			
	ψ(.) p(season*method)	0.08	0.38	0.25	0.08	0.91	0.91	0.91
	Model averaged estimates		0.39	0.25	0.06	0.85	0.85	0.80
	SE		0.05	0.04	0.02	0.10	0.10	0.14
Gray squirrel	ψ(.) p(method)	0.38	0.03	0.12		0.44	0.44	
	ψ(.) p(.)	0.27	0.09	0.09		0.36	0.36	
	ψ(method) p(method)	0.15	0.02	0.12		1.00	0.38	
	Model averaged estimates		0.05	0.11		0.49	0.41	
	SE		0.04	0.04		0.25	0.18	
Cottontail	ψ(.) p(method)	0.76	0.41	0.02		0.35	0.35	
	ψ(method) p(method)	0.20	0.41	0.01		0.34	1.0	
	Model averaged estimates		0.41	0.01		0.35	0.49	
	SE		0.07	0.01		0.17	0.26	
Red fox	ψ(.) p(method)	0.24	0.19	0.04		0.32	0.32	
	ψ(.) p(.)	0.20	0.10	0.10		0.30	0.30	
	ψ(.) p(veg)	0.18				0.52	0.52	
	Model averaged estimates		0.15	0.06		0.35	0.41	
	SE		0.09	0.05		0.17	0.22	

[a] Occupancy modeled as constant (.) across sites or varied by vegetation or detection method; detection modeled as constant across all sample occasions or varied among seasons, vegetation, detection methods, or the interaction of method × season.

[b] Weights (w_i), calculated using the small sample version of Akaike's Information Criterion (AIC$_c$), indicate the relative support for a given model.

[c] A subset of parameter estimates are provided from remote cameras, cubby boxes, and hair traps, but model-averaged and SE estimates are based on the full set of candidate models.

[d] Abbreviations: CAM, cameras; CUB, cubby box; HAIR, hair trap.

indicating that remote cameras had the highest detection probability for most species. Four species (i.e., coyote, cottontail, gray squirrel, and opossum) had evidence of different site occupancy estimates among detection methods, but AIC$_c$ model weights of ψ(method) models totaled only 10–20% among these species. For these species, low detection probabilities by one of the methods in the array resulted in high and questionable occupancy estimates, thereby favoring ψ(method) models. In addition to opossums, we also detected raccoons and skunks by all 3 methods and each one varied widely in its effectiveness (Table 1). As a result, the type of method influenced our ability to detect both of these species (Table 2).

Top model weights indicated that vegetation type had some influence on detection probabilities for striped skunks and red foxes and on occupancy estimates for skunks, raccoons, and opossums (Table 2). Specifically, we did not detect red foxes in pine forests or wetlands, and we detected striped skunks and opossums in all vegetation types except oak forests. Raccoons occurred in all vegetation types with the highest number of detections in wetlands and grasslands. Opossums, and to a minor extent, raccoons showed seasonal differences in detection probabilities (Table 2), but we observed no consistency between these species. The highest detection probabilities occurred in late summer and fall for opossums, whereas higher detection probabilities occurred in the spring for raccoons.

Results from our method-specific analysis suggested that detection probabilities and site occupancy varied among the 9 species detected by remote cameras and the 7 species detected by cubby boxes (Table 3). However, we found no evidence of occupancy differences among the 4 species (coyote, opossum, raccoon, and striped skunk) detected by hair traps. Detection probabilities for hair traps appeared to be influenced by seasonal variation, with detection probabilities higher in Fall 2001, when stations were initiated, compared to later sampling seasons. Model-averaged estimates were $\hat{p}_{\text{Fall01}}= 0.21$ (SE = 0.10) for hair traps, but never exceeded 0.08 in any other season. Species-specific site occupancy estimates were similar to those given in Table 2.

Table 3. Method-specific results from a candidate set of 8 models[a] applied to detection and nondetection data for mammals on Cape Cod, Massachusetts, USA, 2001–2002.

Method	No. of species detected	Models	w_i[b]
Remote cameras	9	ψ(species) *p*(species)	0.93
		ψ(.) *p*(species)	0.07
Cubby box	7	ψ(.) *p*(species)	0.67
		ψ(species) *p*(species)	0.33
Hair traps	4	ψ(.) *p*(season)	0.72
		ψ(.) *p*(.)	0.17
		ψ(species) *p*(season)	0.05

[a] Occupancy probability (ψ) modeled as constant (.) or different among species; detection probability (*p*) modeled as constant across all species or varying among species, seasons, or both (species × season).

[b] Weights (w_i), calculated using the small sample version of Akaike's Information Criterion (AIC_c), indicate the relative support for a given model.

When we addressed a possible lack of independence among detection methods using the most conservative value for effective sample size, we found little effect on model selection. In most cases, the top models for each species in Table 2, including the simpler models with constant occupancy probabilities, had even higher weights of evidence.

Based upon our detection probabilities, remote cameras on Cape Cod need to be deployed ≥12 weeks to confirm coyote site occupancy (with 95% accuracy), whereas hair traps would require over three times the sampling period (Fig. 2A). The probability of detecting a raccoon at least once at occupied sites approached 95% after 6–7 weeks of sampling with remote cameras and 11 weeks with cubby boxes, and it would require >30 weeks with hair traps (Fig. 2B). Using our model-averaged detection estimates for coyotes on Cape Cod as a comparison (Table 2), the optimal number of weeks per year needed to confirm occupancy is 12–15 for remote cameras and >30 weeks for hair traps. The optimal number of weeks needed for raccoon is 6–7 weeks for remote cameras, 8–12 weeks for cubby boxes, and 26–34 weeks for hair traps.

Discussion

Our results indicated that detection is never equal to one nor is it likely to be constant across time or space because behavioral factors, seasonality, density, local environmental factors, sampling designs, and specific methods all can influence detectability (Royle and Nichols 2003, Bailey et al. 2004). The biology and ecology of each species should also be considered when evaluating differences in detectabiltiy and site occupancy. In at least one case, the physical attributes of a species may have influenced detection by our detection methods. For example, long-tailed weasels have long, slender bodies and short limbs, a body shape that probably did not encourage detection via the hair traps and the camera system setups we used. For both sampling methods, modification of designs to better suit small mustelids may increase detection probabilities. Although gray squirrels can easily be detected by remote cameras and are ubiquitous across Cape Cod wherever trees are found, our cameras were operable only from dusk to dawn for logistical reasons, thereby making it unlikely to detect a species that is active primarily during daylight hours. In coastal environments, raccoons often forage in coastal marshes or along nearshore beaches (Ivey 1948, Ratnaswamy et al. 1997). In many coastal systems like Cape Cod, beach communities succeed directly into grasslands where we recorded a relatively high number of detections for raccoons. The sizeable weight associated with the vegetation model (Table 2) supported this finding and suggested that individuals on beaches likely found our grassland sites. Skunks prefer dense vegetative cover and heterogeneous landscapes in association with den sites (Rosatte and Larivière 2003), and although red foxes utilize a variety of habitats, they also prefer diverse landscapes, with forests and woodlands generally constituting less favorable habitat (Lloyd 1975). Thus, it was not surprising that we did not detect these species in many forested sites because local management practices on portions of Cape Cod have encouraged vegetation communities to succeed naturally, resulting in mature forest stands with decreasing plant

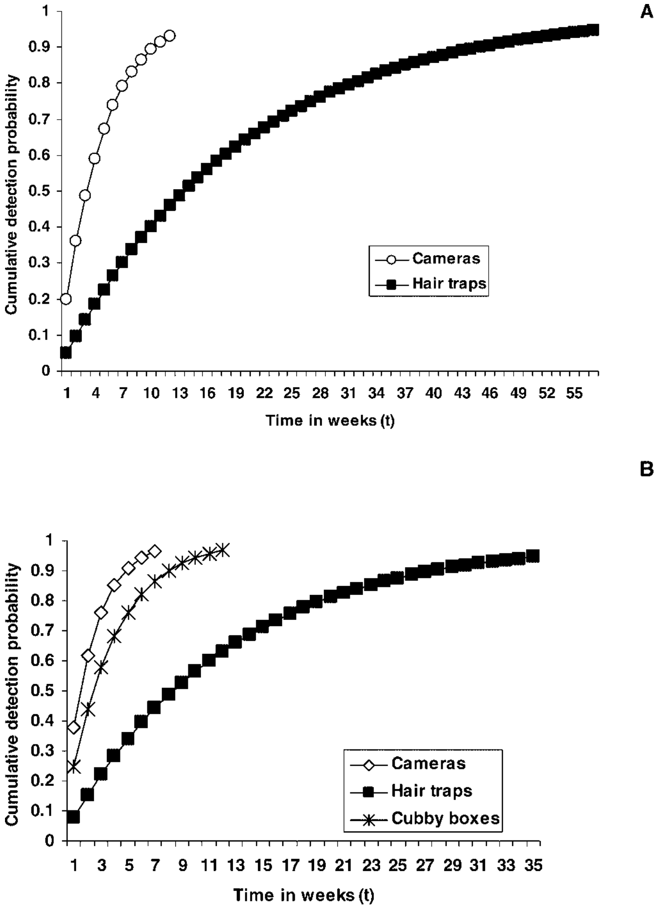

Figure 2. Probability of detecting coyotes (A) and raccoons (B) at least once (cumulative detection probability) in *t* weeks of sampling on Cape Cod, Massachusetts, USA, 2001–2002. Graphs based on model averaged (weekly) detection probabilities for each species and associated detection methods.

diversity. Model weights also indicated a strong seasonal influence on the detection of opossums and supports previous research conducted on this species. Opossums are known to exhibit strong seasonal variation in basic activities like foraging and nest building (McManus 1971), and therefore may have been difficult to detect during colder weather. Although we sampled a small number of sites in each vegetation type (2–3), the weights associated with models containing vegetation for some carnivores suggested that our sample allocation and effort was adequate to distinguish a vegetation influence on detectability or site occupancy. We sampled all the major vegetation communities that occurred in our study area and covered most of the land area available, despite the irregular boundary of federal land ownership.

Remote cameras proved to be the most effective detection method, recording the highest number of species, but cubby boxes were also reasonably effective. In contrast, hair traps performed poorly on all the species that they detected (low detection probabilities), yielding questionable estimates of occupancy rates (Table 1) except for the striped skunk. We used hair traps designed specifically to detect mesocarnivores (Baker 1980) and recommend either design changes suitable for species with similar habits or physical characteristics (e.g., hair traps designed specifically for small mustelids [Mowat and Paetkau 2002]), or higher sampling effort (i.e., more devices) at sites, over longer periods. Overall, species-specific detectability varied considerably among the methods we used, making site occupancy estimates questionable when not accounting for this variation (Table 2). Despite these differences and consistent with our a priori expectations, site occupancy estimates obtained from the different detection methods were similar for some species but imprecise for the rest (Table 1); thus, models with constant occupancy, $\psi(.)$, were favored for all species (Table 2). For example, both remote cameras and cubby boxes effectively detected raccoons. Using unadjusted estimates of occupancy would suggest that this species occurred in fewer sites when sampling with cubby boxes compared to remote cameras, making it impossible to compare studies that employed different methods. However, if detection probability is measured, then adjusted site occupancy estimates are consistent via these 2 methods (Table 1). We attributed consistency in occupancy across methods due to a combination of the raccoon's inquisitive nature, well-developed senses, intelligence, and dexterity with their front limbs that allowed them to find locally available food resources (Gehrt 2003 and references therein) and activate all of our detection methods.

Inferences made from our model selection remained unchanged when we used the most conservative sample size of 13 sites, implying that the use of multiple detection methods at sites did not influence model selection. Although this analysis does not directly assess the effects of a possible lack of independence on precision (i.e., the precision of the resulting estimates could be overstated), it does address the issue of influence on model selection due to inflated effective sample size (MacKenzie and Bailey 2004). The issue of effective sample size and dependence has not been well explored in the context of site occupancy and can also be ambiguous for many capture–recapture studies (Burnham and Anderson 2002). It is likely that the value for effective sample size depends on the parameter of interest (Kendall and Bjorkland 2001, Burnham and Anderson 2002).

Site occupancy surveys that incorporate detection probabilities provide the necessary foundation for conducting effective biological inventories and subsequent monitoring. Occupancy surveys are often used to document species presence and determine their distribution, but there is usually no attempt to estimate detection, resulting in naïve occupancy estimates that are negatively biased by an unknown amount (Bailey et al. 2004). Historically, many of these programs have not considered the influence of experimental design, sampling methods, or local environmental factors on detection. Conversely, inventories and occupancy surveys that collect detection information can serve as a powerful guide for future monitoring or research efforts by establishing an information-base from which scientific inferences can be made. For example, if a method is used that is cost-effective but not the most efficient one for detecting a particular species, detection probability can be used to adjust both the temporal and spatial frame needed to monitor that species. In our sampling of coyotes and raccoons on Cape Cod, the optimal number of weeks to establish occurrence (with 95% accuracy) mimics the time frame needed to verify site occupancy (Fig. 2A,B). The similarity between the optimal number of weeks sampled and the time frame needed to verify site occupancy is due to the fact that both species are fairly common in the target area; in these cases, sampling a small number of sites repeatedly to establish site occurrence may be more efficient than sampling a large number of sites with few repeat surveys (MacKenzie and Royle 2005).

Although we believe that the proportion of sites occupied is useful as a state variable in a monitoring context, it should not be viewed as a universal approach for assessing change in wildlife populations. Current models do not produce valid site occupancy estimates when detection probabilities fall below 0.15. Under this scenario, there is no way to distinguish between where the species is poorly detected compared to true absence (MacKenzie et al. 2002). Data collected under these circumstances (e.g., use of hair traps to sample coyotes, see Table 1) are not suited for use in site-occupancy estimation, and it is particularly important to recognize that the information is flawed, even as a crude index to occupancy. In such cases, some effort should be made to increase detection rates, either through reallocation of sample effort, extending the sample period, or methodological changes. Even previous studies have noted this limitation; the term "visitation rate" often represents a combination of occupancy and detection ($\psi \times p$) and studies have shown that if the value drops below 0.15, the utility of the information to provide inferences is suspect (Moruzzi et al. 2002, Sargeant et al. 2003). Low detection probabilities may be especially problematic for rare species where few, widely distributed individuals are available to be detected or locally enigmatic species have a highly clumped distribution across the landscape. A second caveat is that spatial heterogeneity in either site occupancy or detection probabilities must be accounted for among sites and linked to some covariate information such as site characteristics or local environmental conditions (MacKenzie et al. 2002). Unexplained heterogeneity, although too restrictive for the current models, can be modeled, but it generally requires large numbers of sampling sites (Royle and Nichols 2003).

Management Implications

In the future, pilot studies and monitoring programs will benefit from incorporating estimation of detection probabilities into their design and analysis because of the potential differences in site occupancy estimation when detectability is considered. Investigators can use statistical methods to evaluate the likely impacts (in terms of reduced occupancy precision) of alternative designs that assess precision of estimates for various designs that differ in sampling effort (MacKenzie and Royle 2005). Another possibility would be to use multiple sampling methods at sites to increase detection by modifying the multispecies model presented by MacKenzie et al. (2004). Multiple methods could result in detection at a single site (e.g., a partial detection history of "A0," would indicate that the species was detected by method A, but not method B, during a single sampling occasion). Under this model it should be possible to formally test for detection independence among sampling methods within sites.

One of the great strengths of implementing rigorous statistical designs is the ability to construct composite models that combine information over time and studies to strengthen inference. For example, occupancy studies can be used in combination with related analyses to expand our knowledge of species' relationships and community dynamics. On Cape Cod, both coyotes and red foxes occur, and red foxes have long been of concern to managers as a potential predator of nesting shorebirds. Where the 2 canids co-occur, coyotes can influence the intensity of red fox predation (Sovada et al. 1995), but little is known about their relationship in this coastal system. We suggest that bias-adjusted occupancy estimates and detection probabilities be used to assess co-occurrence patterns, and supplement information collected via other methods (e.g., radiotelemetry) or manipulative experiments to strengthen biological inferences about these populations. Occupancy models provide a convenient framework for such extended analyses, with the qualification that there is some danger in making strong inferences about processes from occupancy patterns alone (MacKenzie et al. 2004)

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