ESTIMATING DENSITY OF COYOTES FROM CALL-RESPONSE SURVEYS USING DISTANCE SAMPLING AND SOUNDSHED MODELS

by

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Abstract

S. J. K. Hansen. Estimating density of coyotes from call-response surveys using distance sampling and soundshed models, 80 pages, 2 tables, 8 figures, 1 appendix, 2013.

Density estimates that account for differential animal detectability are difficult to acquire for elusive species such as mammalian carnivores. I evaluated two novel designs to account for detectability of coyotes (*Canis latrans*) using vocalization surveys: distance sampling and soundshed modeling. This large-scale study involved 524 call-response surveys across New York State, using triangulation to estimate distance to calling animals and estimate the probability of call detection. As an alternative, I propagated sound across the landscape in a GIS to produce a standalone detectability function. Compared to distance sampling, soundshed modeling provided a finer-resolution, spatially-explicit estimate of detection, yielded a slightly lower and more precise estimate of coyote density in the state, and provided a more efficient means of monitoring changes in coyote populations using vocalization surveys. Both approaches are applicable to other vocal species from songbirds to marine mammals, and soundshed modeling in particular may greatly improve the utility of vocalization surveys for population monitoring.

Key-words: *Canis latrans*, density estimation, distance sampling, coyote, New York State, population monitoring, probability of detection, soundshed, SPreAD-GIS, vocalization surveys.

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Introduction

Coyotes *Canis latrans* occupy a broad geographic range, having colonized much of North America following the extirpation of wolves *Canis lupus lycaon* from large portions of their former distribution (Parker 1995). However, coyotes have become common in many regions only within the past several decades, especially the eastern United States. Throughout much of the Northeast today coyotes are considered to be the most abundant and widespread mid-sized carnivore, indicating the capacity for a large and potentially profound impact on the ecosystems they have colonized. Moreover, coyote colonization of the eastern U.S. has generated tremendous public interest, with "how many are there?" being the number one question the public asks the New York State Department of Environmental Conservation. State agencies desire a defensible answer to that question to satisfy the public. Managers also desire an efficient means of quantifying coyote abundance to gauge their potential ecological impacts, direct management action, and evaluate coyote population responses to management action.

The abundance (or density) of a species is a key parameter determining its status and ecological impact (IUCN 2012), but for wide-ranging and elusive animals like the coyote, abundance is also one of the most difficult population parameters to estimate. Increasing the spatial extent of population surveys to provide statewide inferences usually requires a decrease in the local field effort (assuming money and time are an issue); thus, indices of abundance rather than true abundance estimates are typically employed for large-scale monitoring programs. For wild carnivores, especially cryptic animals like the coyote, the number of vocalizations, tracks, or scats encountered per unit effort are commonly used indices of abundance (Henke & Knowlton 1995). For coyotes and wolves, call-response surveys in

particular have been widely employed because these species reliably respond vocally when within hearing distance of a broadcast call (siren or recorded series of howls; Wolfe 1974; Wenger & Cringan 1978; Goff 1979; Sharp 1981; Harrington & Mech 1982; Pyrah 1984; Crawford, Pelton & Johnson 1993; Gaines, Neale & Naney 1995) and these surveys are easily conducted from roads, eliminating reliance on private land access to collect data. Such indices of abundance are useful for monitoring trends in populations when the relationship between true abundance and the index is known, but without establishing and periodically validating that relationship, a change in the index may indicate either a change in the population or a change in the relationship between the index and true abundance. Developing useful indices of abundance therefore must begin with a baseline estimate of true abundance, and more desirable would be an efficient way to turn easy to collect data like call-response rates into a means of estimating population density (and therefore abundance) with precision (Marques *et al.* 2012).

An ideal population estimator for a species like the coyote would be inexpensive, efficient in terms of field logistics, and noninvasive. Furthermore, the estimator would produce confidence intervals with a meaningful degree of precision (20% coefficient of variation being the most common standard; Patel, Patel & Shiyani 2001) and it would be scalable, meaning it would provide reliable estimates within a wildlife management unit, ecoregion, or larger spatial scale. Herein, I provide two novel approaches for estimating coyote density in New York State that meet these conditions. Chapter 1 explores the use of road-based call-response surveys within a distance sampling framework that uses established analytical techniques to estimate both probability of detection and density for a single population. The novelty here lies in using

a triangulation approach to quantify distance to sound rather than to a visually-detected animal. Chapter 2 embarks upon more novel ground by estimating a GIS-based, spatially-explicit standalone model for the probability of detecting coyote calls. This standalone model was used to correct call-response survey counts of coyotes using the same data from the distance sampling effort, but without requiring that distance be estimated.

The chapters in this thesis have been prepared for publication as contributed research papers in the *Journal of Applied Ecology*.

Chapter 1

Pairing call-response surveys and distance sampling for a mammalian carnivore

Summary

1. Precise density estimates that account for differential animal detectability are difficult and costly to acquire for elusive species such as mammalian carnivores. Less expensive indices, e.g. call-response rates may thus be favored for monitoring despite potential unreliability over space and time due to differences in animal detectability. Seeking an efficient and robust means of monitoring an elusive but vocal carnivore, coyote *Canis latrans*, I paired distance sampling with call-response surveys.

2. My approach addressed both non-response bias and call detectability, and I used triangulation (with three simultaneous observers) to determine distance to a calling animal. The approach was field-tested under controlled conditions using staged calls and blind observers as well as GPS-collared animals, and then applied in a broad-scale survey of coyote populations across New York State from June–August 2010.

3. Surveys at 541 points (≥ 6 km apart) yielded 66 responses triangulated to ±119 m precision. The estimated probability of detection for calling animals was 0·19 ± 0·03 SE. Correcting for a 48% non-response rate (probability of availability) in addition to the probability of detecting a calling coyote, I estimated 1·3 coyote pairs 10 km^{-2} (95% CI: 0·8–2·1), reflecting the territory-holding population component based on known patterns of coyote calling behavior.

4. *Synthesis and applications*. Pairing distance sampling with call-response surveys provided an efficient means of monitoring coyotes that is readily extendable to other elusive but reliably

vocal mammals such as wolves *Canis lupus*, golden jackals *Canis aureus*, and some primates. The approach is sufficiently flexible for use at multiple scales and for other species provided the key assumptions of distance sampling are met.

Introduction

Estimating animal density with precision is needed to monitor changes in small or at-risk populations (Joseph *et al.* 2006; Kindberg, Ericsson & Swenson 2009; Antao, Pérez-Figueroa & Luikart 2011), evaluate the ecological impacts of invasive, common or strongly-interactive species (Berger & Gese 2007; Letnic *et al.* 2011), quantify population responses to management actions (Wittmer *et al.* 2005; Mangas & Rodríguez-Estival 2010; Kinnaird & O'Brien 2012), and ultimately facilitate defensible management decisions. With wild species, robust estimates of density are commonly obtained using one of two methods: capture-mark-recapture (CMR; Otis *et al.* 1978) or distance sampling (Buckland *et al.* 2001), both of which estimate and correct for the probability of animal detection during surveys. CMR approaches fundamentally require capturing and marking individuals and resighting marked individuals over time. Camera traps and non-invasive genetic sampling avoid the physical capture requirement, greatly increasing the utility of CMR approaches for highly vagile and hard or risky to capture species like large-bodied mammals. However, camera-based CMR remains available only for species with unique natural markings (Karanth 1995; Trolle & Kéry 2003; Negroes *et al.* 2010), costs for non-invasive genetic CMR remain high due to the large number of samples required, and both camera and genetic methods require a high sampling intensity which renders geographically restricted inferences. In contrast to CMR, distance sampling requires sighting a given animal during point-

or transect-based surveys, and accurately measuring the distance between the animal and the observer. With this approach, the frequency of animal sightings with respect to distance from the observer provides the information needed to estimate the probability of detection and correct animal counts. Distance sampling yields robust population estimates for rare species (Focardi, Isotti & Tinelli 2002; Ellis & Bernard 2005; Zylstra, Steidl & Swann 2010), efficient surveys given both small and large sampling regions (e.g. Andriolo *et al.* 2005; Durant *et al.* 2011), and population estimates from a single sampling event (provided sufficient detections are recorded) making the approach more broadly applicable than CMR for monitoring large animal populations (Samuel *et al.* 1987; Jathanna, Karanth & Johnsingh 2003; Liu *et al.* 2008; Schmidt *et al.* 2012).

Aural detection of animals has extended the utility of distance sampling to hard-to-sight but reliably vocal species like songbirds (Somershoe, Twedt & Reid 2006), cetaceans (Marques *et al.* 2009; Kusel *et al.* 2011), and some primates (Dacier *et al.* 2011). Broadcasting calls to elicit vocal responses can increase detection rates for species that vocalize too infrequently for passive surveys such as marsh birds (Conway, Gibbs & Haukos 2005) and burrowing owls *Athene cunicularia* (Haug & Didiuk 1993). Although several mammalian carnivore species reliably vocalize, e.g. gray wolves *Canis lupus*, golden jackals *Canis aureus*, and coyotes *Canis latrans*, call-response surveys for these species are typically used only to provide an index of animal abundance (e.g. responses per unit effort) rather than a detectability-corrected population estimate (Wenger & Cringan 1978; Goff 1979; Sharp 1981; Harrington & Mech 1982; Okoniewski & Chambers 1984; Blanton 1988; Giannatos *et al.* 2005). Linking the power of

distance sampling to call-response surveys could provide a novel and efficient survey method for monitoring these otherwise elusive carnivore species.

Several assumptions underlie valid inference from distance sampling, reflecting both design and behavioral issues that pose specific challenges to call-response surveys for carnivores. In terms of design, foremost, survey locations must be random with respect to the distribution of the target species (Buckland *et al.* 2001). Large-scale studies of carnivores are typically road-based (Wolfe 1974; Sharp 1981; Fuller & Sampson 1988; Crawford, Pelton & Johnson 1993), and roads may either fail to provide adequate coverage of the ecological conditions pertinent to wide-ranging species (a design issue) or may be avoided by the target species (e.g. Wittmer *et al.* 2005). The process of binning observations into categories of distances to estimate the probability of detection may be sufficiently flexible to accommodate road responses, but some idea of the magnitude and direction of animal responses with respect to roads is necessary. Second, the distance between the observer and the animal must be measured precisely or at least with sufficient precision relative to the width of distance bins required for a precise estimate of the probability of detection (Buckland *et al.* 2001). With long-range vocalizations, estimating distance to the call based solely on call volume is discouraged (Alldredge, Simons & Pollock 2007b) because variation in the volume and direction of the source call (Alldredge, Simons & Pollock 2007a), characteristics of the surrounding landscape (Fricke 1984; Simons *et al.* 2007), and meteorological conditions at the time of survey (Wiley & Richards 1982) will each act to attenuate sound. Thus, some alternative to estimating distance to vocalizing carnivores, like triangulation or passive acoustic arrays, should be considered and their estimation errors quantified. Third, for each detection, the number of

animals present must be counted with certainty. Hallberg (2007) demonstrated that un-aided aural estimation of group size is possible; however, harmonic obfuscation of individual signals within the group combined with sound attenuation processes affect certainty of the count (Lehner 1978; Harrington & Mech 1982). This problem may be overcome by recording animal responses and performing a spectral analysis to identify individual signals (Dawson & Efford 2009; Blumstein *et al.* 2011) or, perhaps more efficiently, using a cue counting approach where each detected response counts as one group and estimates of group size are incorporated into the density estimate as a multiplier.

In terms of behavioral responses, the assumption that all animals directly on the survey line (or point, in this case) must be detected (Buckland *et al.* 2001) may be an issue with territorial carnivores that might not respond vocally to a loud and close call (resulting in non-detection of animals at the survey point). This problem may be alleviated to some degree by starting broadcasts at say half volume and increasing volume over successive broadcasts (Harrington & Mech 1982). Animals also must be detected (and distances to those animals measured) at their initial location. That animals do not move prior to responding vocally in call-response surveys has been rarely tested, and could bias density estimates depending on the direction and magnitude of movement (Fuller *et al.* 2012). Movement could be especially problematic with territorial animals that may investigate the area from which a call originated prior to or perhaps instead of producing a vocalization in response to it (Mills, Juritz & Zucchini 2001; Robbins & McCreery 2003; Fuller *et al.* 2012). Radio-collared or highly visible animals in controlled call-response trials may be required to understand the magnitude of this issue for a given study species. Finally, that not all animals may respond to a broadcast call (Buckland *et*

al. 2004; Bächler & Liechti 2007) creates differences in availability among individuals that might correlate to gender, social status, or proximity to the calling device, any of which could introduce biases that underestimate population size by underestimating the encounter rate (Fulmer 1990; Mitchell 2004). For these reasons, any initial effort to pair distance sampling with a vocalizing carnivore should focus on a species whose responses to call-elicitations have been fairly well studied, and for which ancillary data (e.g. radio-telemetry data) is available to test critical assumptions.

Coyotes provided an ideal study animal for this research because their behavior with respect to call-elicitations has been well studied (Alcorn 1946; McCarley 1975; Goff 1979; Sharp 1981; Lehner 1982; Pyrah 1984; Blanton 1988; Walsh & Inglis 1989; Coolahan 1990; Fulmer 1990; Crawford, Pelton & Johnson 1993; Gaines, Neale & Naney 1995; Gese & Ruff 1998; Dunbar & Giordano 2002; Mitchell 2004; Hallberg 2007), they are generally widespread and abundant throughout the eastern United States (Fener *et al.* 2010), and a companion study in New York State provided access to GPS-collared coyotes to evaluate critical assumptions about their behavior with respect to roads. Herein, I evaluated a novel distance sampling approach using call-response surveys to provide the first comprehensive assessment of coyote population status in New York State. I first evaluated whether roads provided sufficient coverage of ecological variation pertinent to coyotes, and, using the data from GPS-collared animals, evaluated whether coyotes avoided areas adjacent to road-based observation points. I then tested a unique triangulation-based approach to estimating distance to calling coyotes using three simultaneous observers under controlled conditions. Finally, I designed and conducted a statewide population survey for coyotes, using the published literature to account for the

<100% availability of coyotes during surveys, and ultimately estimated the probability of detecting a calling coyote and the size of the statewide coyote population. Ultimately, I demonstrate the utility of distance sampling as a novel means to monitor elusive but vocal carnivores like coyotes over broad geographic scales, and discuss considerations for extension to other species, landscapes, and scales.

Materials and methods

Study area

My study area encompassed ~122,000 km^2 of New York State (excluding Long Island), a landscape dominated by private land (~ 85%) except for within the Adirondack Mountains (Fig. 1.1). The region was ecologically diverse with agriculture-dominated and topographically flat plains along the Great Lakes, the mixed agriculture and forest-dominated and topographically rolling Allegany Plateau in the southern tier, the hardwood-forest dominated and topographically rich Adirondack and Catskill Mountain ranges in the east, and marshy river valleys surrounding the mountain ranges (Bailey 1980). Two focal areas that contained GPS-collared coyotes were located in the western (Steuben County) and eastern (Otsego County) Allegheny Plateau region (Fig. 1.1). Elevation across the state ranged from sea level to 1629 m and temperatures average 20·4 °C in July and -6·3 °C in January (Gesch 2007).

Efficacy of road-based design

I first evaluated whether road-based samples captured the same proportional coverage of land cover classes as the overall landscape. To do so, I reclassified the 2006 National Land

Cover Data (NLCD; Fry *et al.* 2011) into six major types: Forest (Deciduous, Coniferous and Mixed), Pasture, Row Crop, Wetland (Forested and Open canopy), Shrub, and Other (Water, Urban, Suburban, and Barren land) using ArcGIS 10 (Esri, Redlands, California). I then calculated the percentage of each cover type occurring within road-based sample points buffered to 1,800 m (n = 541, see Statewide survey design) and a comparable set of 541 random points. I separately tested differences between road and random points within the Adirondack Mountains given the much lower road density in that region compared to the rest of New York State. Overall, I observed <3% difference in land cover composition between road-based survey areas and random areas in the Adirondacks, and <2% difference elsewhere. I thus considered road-based samples to adequately provide coverage of the ecological conditions pertinent to coyotes in the state. However, I expected coyote density and detectability to differ among urban, suburban, and rural environments and for this study urban and dense suburban areas were eliminated from the statewide sampling.

To assess potential road avoidance behavior by coyotes, I compared habitat use and availability within discrete distance-from-observer categories (distance bins around road-based sample points) using data for 10 GPS-collared coyotes (4 males and 6 females monitored 2007–2009) from my focal areas (Fig. 1.1). I retained one independent location per animal per day (near midnight), from June–August (coincident with my statewide sampling design), yielding 807 GPS locations. I chose three distance bins (0–360 m, 360–720 m, and 720–1080 m), which were deemed useful based on the observed responses from my statewide survey and the accuracy of my triangulation trials. To test for a road bias in coyote distribution, I compared the proportion of coyote locations in each distance bin versus the proportional area of each bin

using a χ^2 test. I repeated this analysis using my triangulated coyote detections from the statewide survey (n = 66) as the sample of used locations to test whether I systematically heard coyotes at frequencies different than expected based on GPS-collared coyote locations.

Call broadcast equipment

My call broadcast unit consisted of two, 50-watt Powerhorn loudspeakers (RadioShack®, Fort Worth, Texas) paired with a Mini Audio Amplifier (RadioShack®, Fort Worth, Texas) connected to a MP300-2G mp3 player (Coby Electronics, Lake Success, New York) via standard audio cables. The two speakers were arranged at a 45 degree angle facing opposite directions and mounted on a base plate (design adapted from Varmint Al 2011). Amplifiers were calibrated to a maximum sound pressure level (SPL) of 105 dB (measured at 1 m) during playback to standardize surveys across broadcast units and crews. When broadcasting calls during surveys the broadcast unit was placed on the shoulder of the road (on the ground) with speakers facing perpendicular to the road direction. This physical configuration and placement allowed calls to be broadcast effectively in both directions while maintaining a consistent volume, and allowed the researcher to be separated from the speakers by a distance of approximately 10 m to avoid hearing damage. My call sequence was a combination of group yip-howls and single animal howls (sound source: Macaulay Library, Cornell University) that lasted 20 seconds and varied in both sound frequency and intensity. I spliced calls together using Audacity® sound editing software (Audacity Team 2009) .

Estimating distance to a calling animal

Prior to conducting formal surveys, I evaluated the precision of locations obtained using a 3-person simultaneous triangulation approach (Zimmerman & Powell 1995). Using my broadcast unit, I conducted blind trials at set calling distances, ranging 250–1000 m away from road-based observers, in a mixed agriculture-forest landscape characterized by gently rolling terrain. Observers were spaced 500-m apart along the road and were informed prior to a call broadcast but did not know from which direction or distance a call might originate. Each observer recorded whether or not they heard the call, and, when heard, they recorded a bearing towards the direction of the sound source using a mirrored and declination-adjusted compass. Locations were solved from two to three bearings using Location Of A Signal software (Ecological Software Solutions LLC 2009). I considered a successful location to have either two bearings that produced an error polygon < 0.01 km^2 or three bearings that crossed. For each trio of observers, I calculated the Euclidean distance between the solved triangulation location and the central observer. I estimated distance from the calling animal to the central observer rather than perpendicular distance to the road because each survey represented a point-based rather than line-transect survey. Following this approach, estimated distances had a mean linear error of ± 119 m (n = 51 successful locations). Note that these tests were conducted during daytime, acoustically less optimal conditions compared to night-time surveys (Larom *et al.* 1997), and thus provided a conservative estimate of location precision for the statewide, night-time sampling.

Assessing animal movement in response to the call broadcast

Previous studies with radio-collared coyotes indicated that movement towards a broadcast call may happen after a vocal response, or may preclude a vocal response altogether, but is not likely to occur before a vocal response is made (Alcorn 1946; Mitchell 2004). Moreover, anecdotal observations of animals approaching broadcast calls indicated a lag time of ≥25 minutes (Alcorn 1946; Coolahan 1990), which was longer than the 9-minute duration of my broadcast surveys. Previous studies indicated that group yip-howls had the greatest probability of eliciting a vocal response from coyotes as opposed to sirens, human-produced howls, and broadcasts of lone howls, (Lehner 1982; Okoniewski & Chambers 1984; Fulmer 1990; Gaines, Neale & Naney 1995; Mitchell 2004) and were less likely to elicit an approach than other stimulus (Mitchell 2004; Hallberg 2007). Because Mitchell (2004) indicated that responses might also vary depending on whether the calling individual was familiar to the responder, I attempted to standardize potential response rates as much as possible by using coyote vocalizations recorded outside of New York. Based on these studies I incorporated group yip-howls into the broadcast sequence, used calls that would not be familiar to any potential responders, and assumed movement responses to be minimal.

Statewide survey design

I limited my scope of inference to the rural portion of New York State, excluding interstate highways and all roads within suburban or urban areas because of sampling difficulties and high ambient noise levels. I expected coyotes to hear and potentially respond to call broadcasts when up to approximately 3 km distant (based on a free field sound attenuation

rate of -6 dB per doubling distance), although I was likely to hear them only to ~2 km distant (based on my triangulation tests that accounted for landscape effects and ambient noise conditions). I further expected that a coyote that responded to a broadcast call once may be less likely to do so a second time within the few hours of my evening surveys. For these reasons I spaced my sampling points ≥ 6 km apart (so a given coyote should hear the broadcast call only once during a bout of surveying), and using this criterion randomly selected 720 potential road-based sampling locations statewide.

Surveys were conducted in summer (June–August 2010), at night (dusk to dawn), and during periods lacking wind (≤5 kph) or precipitation – the most acoustically reliable survey conditions based on previous studies (Wiley & Richards 1982; Larom *et al.* 1997; Lengagne & Slater 2002; Thompson *et al.* 2009). Moreover, June through August has been identified by some studies as a peak coyote vocalization response period (Wolfe 1974; Wenger & Cringan 1978; Okoniewski & Chambers 1984).

To provide adequate temporal and spatial coverage across the state, I simultaneously deployed three field crews of three observers each. One observer was placed at the central survey location and was responsible for call broadcasting while the other two observers were stationed 500-m down the road in alternate directions from the central observer. Observers communicated via hand-held radio to synchronize survey start and end times. After arrival at the site, a 2-minute silent acclimatization period allowed for detection of spontaneous vocalizations and helped disassociate human noise from the playback session. For each survey, a series of three call cycles were broadcast, with each cycle consisting of the 20-second call followed by a 2-minute silent listening period. The first 20-second call was played at a SPL of 95

dB and subsequent calls were played at 105 dB (both measured at 1 m, the latter representing the approximate SPL of a coyote howl; Mitchell *et al.* 2006). When a response was detected, the broadcast call was stopped, observers noted the time, estimated the number of coyotes responding, took a compass bearing to the response, and noted their location with a GPS unit. Each observer assigned a qualitative estimate of call quality and ambient noise to aid in interpretation of triangulation results. After all data collection was completed and before moving to another location, the number of animals determined to be calling during that survey was reached by consensus of all observers. In the case where more than one coyote group responded during a survey, observers recorded bearings to all responses and came to consensus on the number of responding groups and number of animals within each. In all cases where a second response was heard and successfully triangulated (n=3), the estimated location was in a different direction from that of the first, with no overlap of error ellipses.

At each survey point, crews recorded both static (land cover, terrain complexity) and dynamic survey conditions (temperature, wind speed and direction, moon visibility, cloud cover, and barometric pressure) that may influence coyote call propagation and detectability. The percent of each of the six previously defined land cover classes were recorded within a 1,800-m buffer centered on each survey location. Barometric pressure at the time of each survey, and 6 hours prior, was estimated by kriging hourly data from 110 weather stations located in and around New York (National Oceanographic and Atmospheric Administration 2010). Moon visibility and the timing of moonrise and moonset were documented using data from the U.S. Naval Observatory (2010). Cloud cover was estimated visually in increments of

25%. Wind speed and direction and ambient temperature were recorded with a Kestrel 2000 weather meter (Nielsen-Kellerman, Birmingham, Michigan).

Statistical analysis

I used Distance 5·0 Release 2 (Thomas *et al.* 2010) to estimate the probability of coyote detection ($\hat{p}$) and density of coyotes within the surveyed areas. Though group size was estimated for each detection, uncertainty in counts occurred when more than three animals were responding. Field personnel also found it difficult to separate pups from adults later in the field season. Importantly, data from Mitchell (2004) indicated that territorial adults are much more likely to respond to a call than transients (~48% response rate for territorial adults vs. ~12% for transients). I thus chose to use a cue counting approach and assumed each detection represented a single territorial breeding pair. I estimated a pooled probability of detection, assuming detectability to be consistent statewide, although I did test for survey covariate effects (barometric pressure, could cover, moon visibility, wind, temperature, and qualitative ambient noise level) on $\hat{p}$ using the multi-covariate engine within Distance. Alternative curves were fit to the probability of detection with the best model selected using Akaike's Information Criterion (AIC; Burnham & Anderson 2002).

A separate issue from the probability of detection is the probability of availability, i.e., what percentage of coyotes that hear broadcast calls are likely to reply vocally (call response rates). Estimates of call response rates have been obtained previously using known (radio-collared) animals and call playback devices. Published response rates range from 0·42–0·55, and average 0·48 (Fulmer 1990; Mitchell 2004). A probability of availability, P_v, less than 1

violates a critical assumption for distance sampling that can be corrected using a multiplier to obtain to final density estimate (Thomas *et al.* 2006). The multiplier acts as a scaling factor on the overall density estimate. Inclusion of a multiplier in Distance requires an estimate of precision that I could not meaningfully estimate from the two published records of call response rates. As a conservative alternative, I conducted a post-hoc correction by dividing the coyote density estimate by the mean response rate (0·48), the upper confidence limit by the lowest published response rate (0·42), and the lower confidence limit by the highest response rate (0·55).

I thus produced a detectability- and availability-corrected estimate of the statewide density of coyotes. I evaluated whether my design had sufficient power to detect regional differences in coyote abundance by stratifying the density estimate among five ecoregions generalized from a GIS layer produced by The Nature Conservancy (Bailey 1997). Ultimately, the total abundance of breeding coyote pairs was calculated by multiplying the statewide density estimate by the total rural area of New York State (109,000 km^2, excluding urban and suburban areas as identified by the NLCD).

Results

I completed a total of 541 point surveys statewide, detecting coyote responses at 92 sites (Fig. 1.1). Of these, I recorded seven spontaneous calls with the remaining animals responding with equal frequency among the three call cycles of the broadcasts. Triangulations failed to resolve a location for 17 of the calls detected, commonly when only two observers detected a response that was either barely audible or suffered from topographic interference

(signal bounce). Removing the 17 failed triangulation attempts yielded a sample size of 524 valid surveys and 75 call detections for analysis. The estimated distance between calling coyotes and the central observer were binned into intervals of 360-m to accommodate triangulation error and truncated to 1,800 m to improve model fit (removing an additional nine responses). Collared coyotes did not demonstrate any bias in their distribution with respect to road-based observation points (χ^2 = 1·5, *df* = 2, *P* = 0·47; Fig. 1.2a), and so no further adjustment of distance bins was required. Moreover, the frequency of coyotes detected in each distance class during surveys was similar to that observed for GPS-collared animals (Fig. 1.2b), indicating that movement in response to the broadcast calls was not apparent. The most parsimonious model for $\hat{p}$, a half-normal function with no adjustment terms (Fig. 1.3a,b), slightly outperformed a uniform model with two adjustment terms and an unadjusted hazard-rate model (ΔAIC = 1·41–1·73). Including site and survey covariates failed to improve model fit, although sample size may have precluded detecting such effects. The half-normal model estimated $\hat{p}$ = 0·19 (0·03 SE, 95% CI: 0·15–0·25), with an effective detection radius of 790 m.

From the raw counts of animals detected, average group size was 1·8 coyotes per response (SE = 0·15) and ranged 1–6 animals. Treating each call as representing a single breeding pair and using a cue counting approach overcame group size uncertainty and helped clarify the scope of inference to territorial pairs. The pooled, detectability-corrected estimate of coyote pair density, before correcting for coyote availability, was 0·63 pairs 10 km^{-2} (95% CI: 0·45–0·90, 20·1% CV). Adjusting for availability (P_v = 0·48) increased the density estimate to 1·3 pairs 10 km^{-2} (95% CI: 0·8–2·1) resulting in a statewide population estimate of 14,310 coyote pairs (95% CI: 8,719–22,887). With only 5–21 detections in each ecoregion, the statewide

survey design lacked the power to detect statistically significant differences in coyote density at a scale smaller than the entire state.

Discussion

Pairing vocalization surveys with distance sampling provided an efficient and robust means of monitoring an elusive but vocal carnivore, the coyote, a species whose abundance is of considerable interest and for which traditional means of estimating animal abundance remains impractical. My approach yielded reasonably precise estimates of animal density (17·9% CV), and given the efficiency of the design was able to deliver a statewide assessment of coyote population status in New York. I limited my scope of inference to resident, territorial coyote pairs because, although the data remain sparse, previous studies indicate that transients rarely if ever respond in call-response surveys (Wenger & Cringan 1978; Fulmer 1990; Mitchell 2004). Gese and Ruff (1998) investigated spontaneous vocalization rates, as opposed to those elicited by a broadcast call, and reported that transient animals were consistently non-vocal as well. Importantly, territories are likely most stable during summer (the pup-rearing period) and territory size, and by extension territory density, is reflective of local habitat quality. Thus, monitoring territorial coyote pairs in summer may best represent the long-term carrying capacity of the landscape. However, local habitat quality will also affect pregnancy rates, pup production and survival, and so local densities of coyotes may vary more than indicated by the density of coyote pairs. Nevertheless, territorial pairs are the population segment driving annual changes in coyote numbers through reproduction and distance sampling for breeding adults linked to a measure of pup production (e.g. den counts) should efficiently track changes

in total population size. Importantly, using distance sampling to correct for differential detectability of calling animals allows managers to track changes in populations with more certainty, providing a powerful new tool for monitoring elusive carnivore populations.

The difficulty of estimating coyote density using more traditional survey techniques has led to few published density estimates, limiting my ability to compare coyote density among regions or contrast accuracy and precision among different methodologies. For example, my estimate of coyote pair density was 1·6–5·7 times lower than summer density estimates from western states (Wyoming, Camenzind 1978; Montana, Pyrah 1984) and provinces (Alberta, Bowen 1981) acquired using den counts and telemetry methods. However, gross differences in scale alone between these former studies (~96–1,243 km^2) and ours (109,000 km^2) may account for the observed magnitude of difference in coyote density. Importantly, a distance-sampling approach provides a more cost-effective method for monitoring changes in coyote numbers compared to telemetry-based, noninvasive-genetic, or CMR approaches, and thus opens the door to increasing our understanding of the spatio-temporal dynamics of coyote density, its drivers, and population responses to management actions.

Given my large-scale sampling design, which resulted in only 5-21 detections per ecoregion, I was unable to quantify regional differences in coyote detectability and instead estimated a single pooled detection probability. Estimating a separate detection function for say the gently rolling and sparsely forested Lake Plains separate from the rugged and densely forested Adirondack Mountains would require acquiring approximately 60-80 detections in each region. If these regions vary in call detectability, which they probably do, then a stratified or area-specific detection function would improve the accuracy and precision of density

estimates. Adaptation of the approach to smaller geographic extents would require a minimum of 10–20 independent sampling stations and, again, a sufficient number of detections to produce a precise density estimate (Buckland *et al.* 2001). In a given evening, I recommend sampling locations be spaced ≥ 6-km apart to insure sampling independence given that coyotes may hear and respond to a broadcast call up to 3-km distant but we are likely to hear that response only within 2 km. For smaller study areas repeated sampling of locations over time will likely be required, and these samplings should be spaced apart in time to avoid habituating resident animals to the calling device (Wolfe 1974; Mitchell 2004).

Applying my approach to other settings (e.g. suburbia) or time periods (e.g. winter, when harvest and dispersal occurs), or extending the scope of inference to the total population (including transients) poses additional challenges. Aural surveys are much more challenging in urban and peri-urban environments where high ambient noise levels result in decreased detection rates (Patricelli & Blickley 2006; Pacifici, Simons & Pollock 2008; Pohl *et al.* 2009). Moreover, in suburban areas, substantial interest from local authorities and others sensitive to close proximity carnivore vocalizations can hinder survey efforts. Conducting vocalization surveys during different seasons would require additional information to account for seasonal variation in call response rates as well as differences in sound attenuation rates, and therefore call detectability. For coyotes, wolves, jackals, and canids in general, most social "reorganization" occurs during the late fall to early winter period when juveniles disperse and survivors find a mate and establish a new territory (a status likely to respond to a call) or remain transient (a status not likely to respond to a call). Importantly, even in rural areas

anthropogenic influences, such as hunting using commercial game callers, may decrease vocal responses by animals.

Of particular interest to game managers is the contribution of transient animals to population density estimates. Given the low vocal response rates observed for non-resident coyotes in previous studies (Fulmer 1990; Gese & Ruff 1998; Mitchell 2004), transient contributions to overall density are unlikely to be quantified using vocalization surveys. However, studies of coyote social ecology in fall have found that transients generally comprise a relatively small proportion of the total population (9%–15%; Camenzind 1978; Andelt 1985; Gese, Rongstad & Mytton 1989), although their numbers may be dependent on local prey availability and harvest pressure. Though transients are an important component of a true population estimate, territorial pairs are the drivers of local changes in density. If identification of population trends over time were the main objective, the fact that transients are likely not represented by my approach would indeed be an asset rather than a limitation.

Beyond ecological challenges, the most "expensive" part of my survey design was the need for three observers to triangulate to a calling animal. Ongoing work aims to remove this limitation by modeling a spatially-explicit, standalone probability of detection model based on sound attenuation. Such a model would enable a fine-scale spatially-explicit estimate of detectability, and by extension a spatially-explicit estimate of density, even from a broad-scale survey design such as ours. Nevertheless, distance sampling via triangulation to calling animals provides an efficient means of monitoring elusive, non-individually identifiable, and wide-ranging carnivores with more certainty than has been previously available. This approach should be readily extendable to other reliably vocal species provided responses to call

elicitations are either well known or can be quantified to insure distance sampling assumptions are reasonably met.

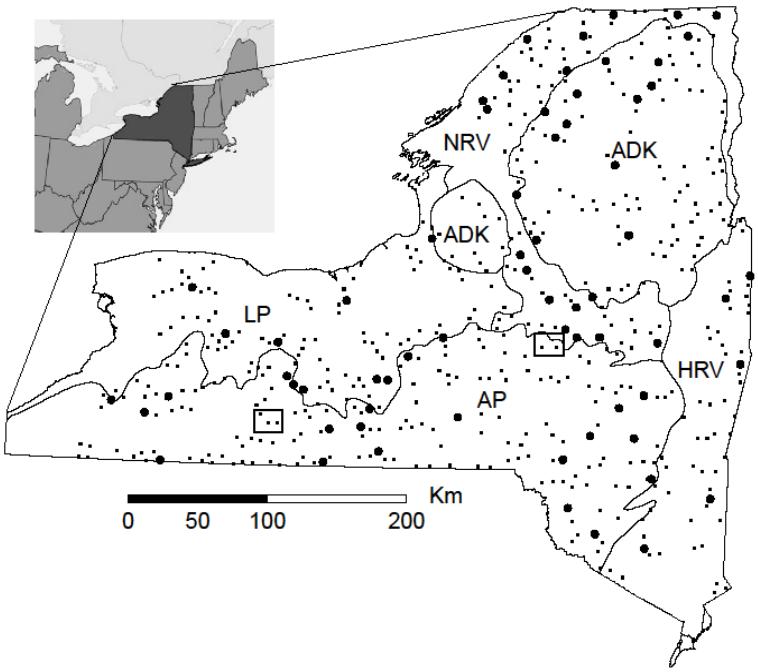

Figure 1.1. The study area for coyote distance sampling in New York State. Map indicates generalized ecoregions (LP = Lake Plains, AP = Allegheny Plateau, NRV = Northern River Valleys, ADK = Adirondack Mountains, HRV = Hudson River Valley), focal study areas containing GPS-collared coyotes (boxes), and survey locations and outcomes (● coyote response detected, ▪ no coyote response detected).

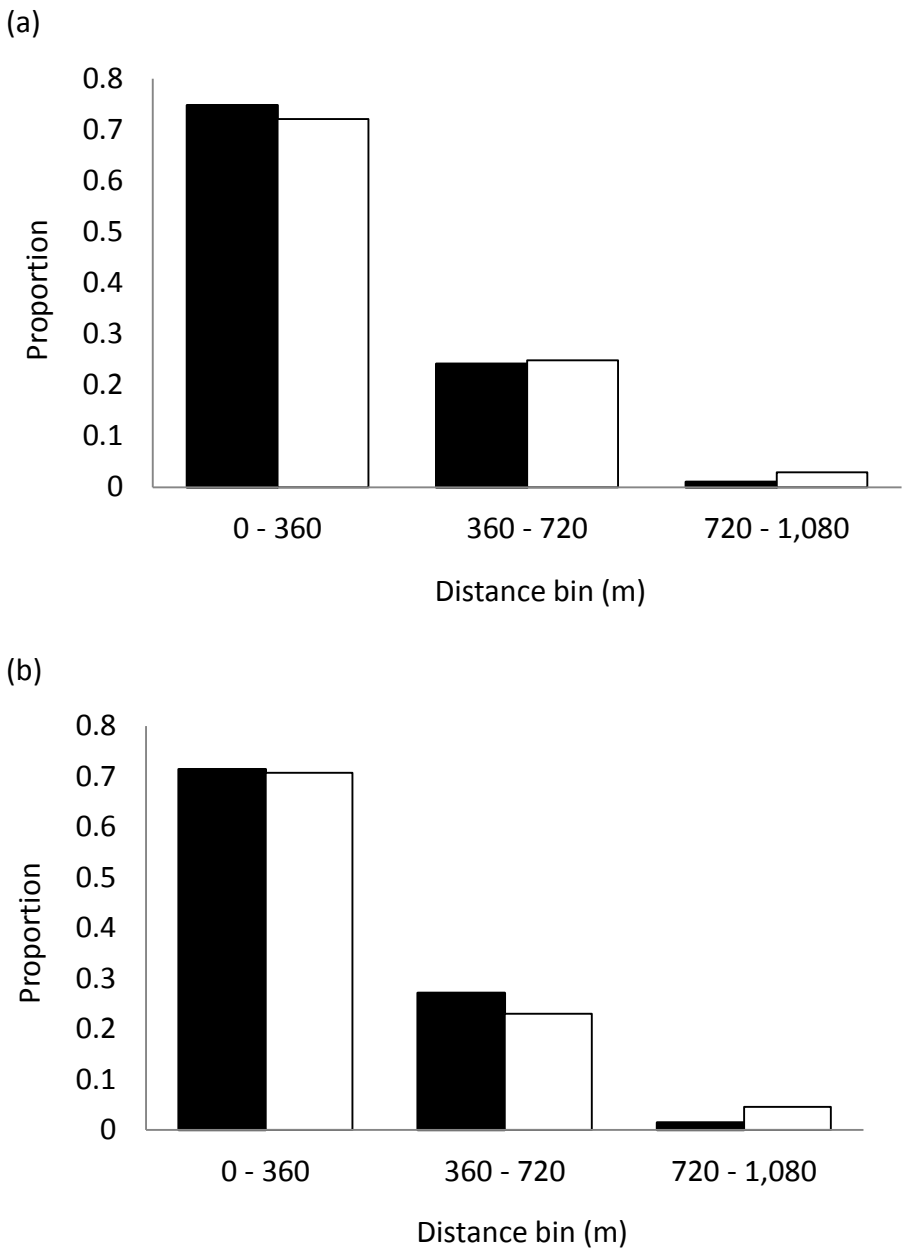

Figure 1.2. Proportion of coyote locations (dark bars)and available habitat (white bars) within specific distance categories away from road-based observation points for (a) GPS-collared coyotes and (b) triangulated survey responses ($\chi^2 = 1{\cdot}5$, $df = 2$, $P = 0{\cdot}47$). Distance categories for point-based surveys include areas along the road as well as away from it.

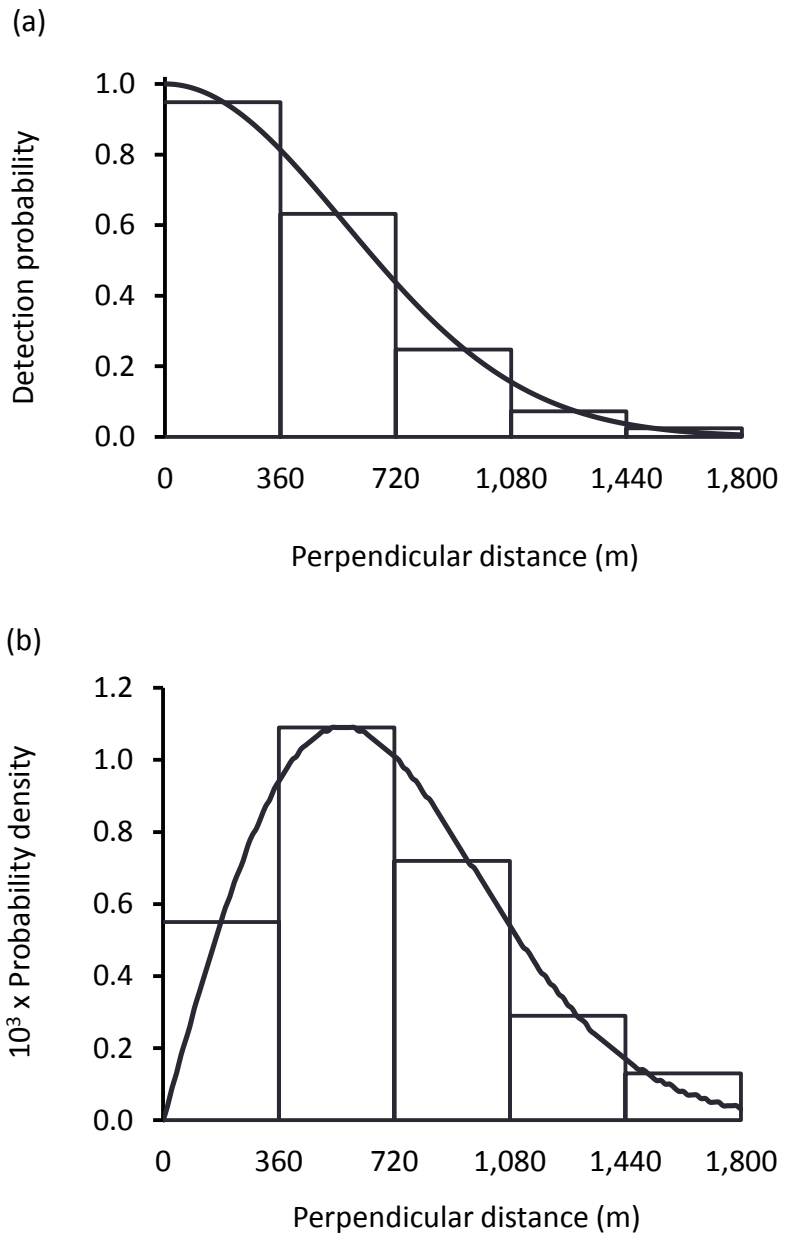

Figure 1.3. (a) Probability of detecting a vocalizing coyote ($\hat{p}$) by distance from observer (m) for road-based coyote vocalization surveys in New York State, June to August 2010 (n = 66 coyote responses). (b) Probability density function showing the relationship between density and area surveyed for a point

Chapter 2

Modeling a spatially-explicit probability of detection for call-based animal surveys

Summary

1. Vocalization surveys are commonly used to provide indices of animal abundance, and when paired with distance sampling may provide a detectability-corrected estimate of actual animal abundance with precision. Distance sampling for animals detected aurally rather than visually poses unique sampling challenges because estimating distance to a sound source based on perceived sound quality alone is unreliable due to the interactive effects of land cover, terrain, and ambient noise on sound quality. Hansen (2013) overcame this limitation using a triangulation approach for coyotes that, although successful, would be logistically challenging for routine monitoring.

2. Herein, I remove the need for estimating distance altogether in vocalization surveys by creating a spatially-explicit and standalone model for the probability of detecting a vocalizing animal based on the physics of sound propagation over heterogeneous landscapes. The model was parameterized for coyotes *Canis latrans* in New York State for comparison to the distance sampling approach of Hansen (2013).

3. I used SPreAD-GIS to evaluate whether the sound propagated from a hypothetical calling coyote would be detectable by an observer at a given distance. Model predictions were validated in blind field trials and then applied to 101 sampling locations statewide. For each location I calculated the probability of detecting a calling coyote, $\hat{p}$, as the proportion of 198 random calls originating within 2 km of a central observer that reached the observer and

remained above ambient noise levels. Site-specific $\hat{p}$ values were then regressed against a suite of terrain and land cover variables to produce a statewide, spatially-explicit and standalone model of $\hat{p}$ used to correct the vocalization counts of Hansen (2013).

4. Field tests indicated high correspondence between empirical and modeled coyote detectability (Cohen's W = 0·88, P < 0·01). The standalone model yielded a mean $\hat{p}$ = 0·27 (2·7% CV), which was significantly larger and more precise than the pooled distance sampling estimate of Hansen (2013; $\hat{p}$ = 0·19, 13·5% CV). Applied to call-response surveys, the standalone model produced a slightly lower and considerably more precise estimate for coyote density than did distance sampling, and indicated regional trends in abundance previously masked by the statewide distance sampling approach.

4. *Synthesis and applications.* Modeling sound propagation based on first principles enabled a standalone, and spatially-explicit estimate for detectability of animal vocalizations. With such a model, a single observer need record whether an animal is heard (and how many) without the complication and uncertainty associated with estimating distance to the calling animal. The approach is broadly applicable to a range of species from songbirds to marine mammals and reliably vocal terrestrial mammals, greatly expanding the utility of vocalization surveys for monitoring animal populations.

Introduction

Population estimates have long been the focus of wildlife managers trying to determine where best to allocate their limited time and resources. Estimates of animal abundance or density serve as valuable benchmarks for informing management decisions and gauging

population response to management actions. Given the uncertain status of many species, widespread declines in habitat area or quality, and ever-tightening budgets for conservation, greater precision and efficiency in population estimates become increasingly important. Yet the cost and geographic restrictions associated with actual population estimates, which require counts of animals to be corrected by an estimate of animal detectability, lead many managers to rely on more easily obtained estimates of relative abundance. However, the detectability of animals may vary over space and time (Bibby & Buckland 1987; Buckland 2006; Marques *et al.* 2010), and without correcting for detectability managers cannot know whether differences in index values represent real differences between populations or differences in animal detectability alone.

Methods to correct raw counts of animals for those missed during a survey generally involve some form of double-counting (Seber 1973), standalone sightability models (Samuel *et al.* 1987), capture-mark recapture methods (CMR; Otis *et al.* 1978), or distance sampling (Thomas *et al.* 2010). For studies that commonly rely on the aural detection of animal presence, e.g. cetacean and bird surveys (Buckland 2006; Marques *et al.* 2009), distance sampling has proven especially useful. Recently, distance sampling has been successfully applied to vocalizing terrestrial mammals such as African forest elephants *Loxodonta Africana cyclotis* (Thompson *et al.* 2009), titi monkeys *Callicebus discolor* (Dacier *et al.* 2011), and coyotes *Canis latrans* (Hansen 2013). An important assumption for the use of distance sampling is precise measurement of the distance between the calling animal and the observer. Alldredge, Simons and Pollock (2007b) demonstrated that distance estimates based solely on perceived sound quality may be grossly biased, yielding estimates that over- or under-estimate

population size depending on whether distance errors are biased toward or away from the observer. Recent technological and analytical advances have allowed researchers to improve distance estimates for songbirds using small microphone arrays and individual song signatures in a spatially explicit capture-recapture approach (SECR; Dawson & Efford 2009). In a larger-scale study involving a vocal carnivore, three simultaneous observers were used to triangulate on calling animals (Hansen 2013). Although successful, these approaches may remain logistically infeasible or cost-prohibitive for routine population monitoring. To the best of my knowledge, standalone detection models have not been employed in acoustic surveys despite considerable knowledge of the properties governing sound propagation that could be exploited to develop such a model.

Although the physics of sound propagation and its role in detecting vocalizing animals have been studied across a spectrum ranging from low-frequency callers such as elephants and cetaceans (Langbauer *et al.* 1991; Thompson *et al.* 2009) to high-frequency callers such as songbirds (Wiley & Richards 1982; Schieck 1997; Hobson *et al.* 2002; Alldredge, Simons & Pollock 2007a; Dawson & Efford 2009), little research has been done to explicitly model sound attenuation over heterogeneous landscapes for use in call-based surveys. The rate at which sound attenuates over space is determined by several highly localized factors that can be used to predict the acoustic qualities of an area of interest. The main factors affecting attenuation are spherical spread (given a -6 dB decrease per doubling distance), absorption by the atmosphere, and reflection by vegetation or other interceding landscape features. Topography can serve as an outright barrier to sound but also may enhance the distance sound travels depending on the elevation of the sound source relative to the receiver (Marten & Marler 1977;

Embleton, Piercy & Daigle 1983; Forrest 1994). Porous ground substrates such as leaf litter, tilled fields, or even a fresh blanket of snow may dampen sound propagation (Marten & Marler 1977) whereas compacted surfaces (e.g. roads, trails, playas, or bare rock) may enhance propagation (Forrest 1994). Humidity and ambient air temperature affect the absorption of sound differently depending on sound frequency (Harris 1966), and wind can cause sound to become highly directional (Thompson *et al.* 2009). Moreover, the signature of animal vocalizations can be swamped by the din of surrounding noise (Wiley & Richards 1978), such as the rush of rivers and streams, traffic-related noise along roads, or the cacophony of other vocalizing animals. For these reasons, sound attenuation patterns are highly heterogeneous, affecting an observer's ability to detect a calling individual and judge distance to that calling individual. While the physics of sound attenuation are well understood, the complexity of modeling these influences over heterogeneous landscapes has likely curtailed creation of standalone and spatially-explicit sound detection models.

Recently, the System for the Prediction of Acoustic Detectability was adapted to incorporate spatially explicit land cover, terrain, and local weather data into predictions of sound propagation from a given location (SPreAD-GIS; Reed, Boggs & Mann 2012). The original application modeled the propagation of vehicle-related noise from roadways into adjacent natural areas. Herein, I used the tool to model sound propagation from vocalizing animals within the range of human hearing to a centrally located observer to calculate the probability of detecting animals in call-based surveys. I parameterized the acoustic properties of the model for coyotes within New York State, and contrasted estimates of the probability of detecting a

calling coyote ($\hat{p}$) and consequent coyote density estimates from call-based surveys that employed distance sampling (Hansen 2013) versus my standalone call detection model.

Materials and methods

Study area

Empirical field trials of sound detectability were completed during summer 2010 at the Carlton Hill Multiple Use Area in western New York State, U.S.A. (42˚50'45"N, 78˚09'04"W). The area was typical of the Southern Tier of New York state, with rolling hills (370–470 m elevation) covered by a mix of deciduous forest and agricultural lands. I ultimately modeled sound propagation across New York State, throughout the Southern Tier as well as the forest-dominated and rugged terrain conditions of the Adirondack and Catskill Mountains, the patchy forest and rolling landscapes of the Hudson Valley, and the agriculturally-dominated and topographically-flat Lake Plains (see Hansen 2013 for full study area description).

Modeling sound propagation

Animal vocalizations may be complex, exhibiting a wide range of frequencies and sound pressure levels. To understand these patterns for coyotes, I used Raven Pro software (Cornell Lab of Ornithology, Ithaca, New York) to perform a spectrograph analysis of a splice of several recorded coyote calls from the Macaulay Sound Library at Cornell University. This spliced call sequence was used in the call-response surveys for coyotes by Hansen (2013). The spectrograph analysis indicated a dominant frequency of 1 kHz. I further assumed the sound pressure level (SPL) of a vocalizing coyote to be 105 dB (measured at 1 m) as reported by

Mitchell *et al.* (2006). These values were the fixed sound inputs for SPreAD-GIS (Reed, Mann & Boggs 2010), a freeware tool available for ArcGIS 10 (ESRI, Redlands, California). Other fixed inputs for SPreAD-GIS included temperature (°C) recorded during field surveys using a Kestrel 2000 weather meter (Nielsen-Kellerman, Birmingham, Michigan) and relative humidity acquired from the closest available weather station (weatherspark.com) corresponding to the timing of the survey. Wind measurements were uniformly set to zero due to the need to apply a single averaged value to all points. Variable landscape inputs to SPreAD-GIS included 2006 National Land Cover data (Fry *et al.* 2011) and a 1-arc-second Digital Elevation Model (DEM; Gesch 2007) resampled to 30 m resolution.

SPreAD-GIS modeled the propagation of sound out from the sound source, producing a continuous grid to a specified distance threshold. Grid output values indicated the SPL (in dB) reaching each cell. Following Reed, Mann and Boggs (2010), land cover values were used to evaluate ambient noise levels within each cell. Assuming light or no wind, I estimated ambient noise SPLs in the range of 18–24 dB (see Appendix I). Final SPreAD-GIS output values were the predicted audible sound levels in excess of ambient noise conditions. I assumed that any non-zero grid value represented a detectable animal call by a human observer located at that cell.

To better represent the actual area sampled around a given survey point (i.e. the area within which I could generally expect a coyote to hear a broadcast call) and standardize sample area across all points, I used sound models from 88 survey locations to estimate a maximum expected sound detection threshold radius. A cumulative distribution curve of the resulting radii indicated that 98% of all broadcast calls would propagate out to no more than 2 km. This

2 km threshold was thus used to establish a constant sample area for all subsequent propagation models.

Empirical test of SPreaD-GIS for animal calls

To empirically validate SPreAD-GIS predictions, I conducted 132 blind field trials involving six observers and 28 fixed call locations. Assuming the maximum distance to which humans may hear a calling coyote to be 2 km, call locations were selected from a grid of possible points spaced 250-m apart to a maximum distance of 2 km. Observers were stationed at 500-m intervals along a road running through the center of the grid (Fig. 2.1a). From a given grid point, technicians equipped with a call broadcast unit played a series of lone howls and group yip-howls for a 20-second duration. The call was broadcast twice from each location, and road-based observers recorded whether they heard the call. Observers knew when the call was being played but did not know the direction or proximity of the technician playing the call. I assigned a value of 1 when a call was detected, and 0 otherwise.

For comparison, the SPreAD-GIS model was run from each of the 28 fixed call locations using temperature recorded in the field and the sound parameters specified previously (Fig. 2.1a). For each trial, I recorded whether each observer was predicted to detect the calling animal at the observation point (assigning 1 given dB value above ambient levels, 0 otherwise). Modeled and empirical detections were compared using the Cohen's *W* correlation coefficient.

Spatially-explicit probability of detection for sound

Calculating $\hat{p}$ at a given survey location required modeling the propagation of sound from all possible calling coyote locations to a central observation point. To accomplish this, I overlaid a hexagonal grid with cell center points spaced 250 m apart on a given survey site to yield 198 equally-spaced potential coyote locations within hearing distance of the central observer (Fig. 2.1b). For each of the 198 locations, SPreAD-GIS modeled the soundshed, i.e. all cells within hearing distance of the fixed sound source where sound levels remained above ambient noise. I recorded a "detection" at the central observation point when a given soundshed overlapped the observer (and recorded a non-detection otherwise). I calculated a soundshed estimate of detection probability ($\hat{p}_s$) as the number of recorded detections / 198 attempts. It should be noted that the area within which a broadcast call could be expected to be heard and responded to may not reach all 198 potential response points. However, this difference in "elicitation soundshed" (i.e. the area around a call-response survey location within which an animal can hear the broadcast call and therefore potentially respond) between individual points should not greatly affect point specific density estimates assuming that the ratio of $\hat{p}_s$ to area sampled remains constant. Situations in which that ratio is not constant (i.e. modeled "responses" are identified as "detected" within the 2 km sample area but fall outside of the actual elicitation soundshed of the survey location) require further investigation but are expected to be minimal based on preliminary analyses.

To create a standalone model of $\hat{p}$ for comparison to the distance sampling approach of Hansen (2013) required estimating $\hat{p}$ at 541 actual coyote survey locations across the state of New York. However, using SPreAD-GIS to model the soundshed from a single location required

2 minutes to complete (roughly 6 hours per location to estimate $\hat{p}_s$). This, modeling the soundshed for all 541 locations appeared time prohibitive, so I decided to model a subsample of locations and use raster calculations to predict detection at a larger set of points. I undertook this in two stages, first calculating $\hat{p}_s$ at a sample of survey locations that varied in terrain complexity and land cover conditions (n = 101 locations), including sites where coyotes were detected (n = 59) and sites where coyotes were not detected (n = 42) by Hansen (2013). I regressed $\hat{p}_s$ values from the 101 modeled survey locations against a suite of landscape metrics to produce a predictive model for $\hat{p}$ applicable to any potential survey location. Candidate models included combinations of terrain ruggedness (percent coefficient of variation of elevation), proportion of area forested, elevation of the observer location, and ecoregion along with second-order polynomial terms (to allow non-linear relationships) and interaction terms for terrain and elevation, and terrain and ecoregion. For this analysis, GIS datasets (composed of 30-m continuous grids) were resampled to 90 m to decrease processing time. Landscape metrics were quantified within a 2-km radius buffer around the central survey location, as well as a 1-km buffer representing nearby effects only, using neighborhood analyses in ArcGIS to compare radii using AIC. I fit beta-logistic models (Kieschnick & McCullough 2003; Ferrari & Cribari-Neto 2004; Buis, Cox & Jenkins 2011) using betafit in Stata 9 (StataCorp 2005), and compared candidate models using Akaike's Information Criterion (AIC; Burnham & Anderson 2002). Goodness-of-fit of the most parsimonious model was assessed using Wald's Chi-square statistic. For clarity, I denote regression model predictions using $\hat{p}_r$.

Comparison of distance sampling with stand-alone detection model

Using the most parsimonious regression model, I predicted $\hat{p}_r$ for each 90-m cell in New York State, and extracted $\hat{p}_r$ at the 524 survey locations of Hansen (2013), which included 66 sites where coyotes were detected in the 2010 field surveys. Following Hansen (2013), I considered all detections of coyotes (irrespective of the total number heard) to represent a single breeding pair. Using the standalone model for detectability, I calculated the density of coyote pairs as:

$$\widehat{D} = \frac{\sum_{i=1}^{n} \left(\frac{1}{\hat{p}_r}\right)_i}{a * k} \qquad \text{eqn 1}$$

where *n* = total number of detections across all surveys (assuming each represents a breeding pair), $\hat{p}_r$ = the probability of detection at site *i*, *a* = area sampled at each point (12.6 km^2 based on 2-km radius), and *k* = number of points sampled (524). The standard error for the density estimate was calculated using the delta method (Seber 1973) as:

$$se(\widehat{D}) = D * \left\{ \frac{se(n)}{n} + \frac{\sum_{i=1}^{n} \frac{se(\hat{p}_r)_i}{\hat{p}_{r_i}}}{n} \right\}. \qquad \text{eqn 2}$$

To make these estimates comparable to those derived from distance sampling, I accounted for the probability of availability (i.e. what percentage of coyotes that hear broadcast calls are likely to respond vocally) using the values and approach reported by Hansen (2013). This entailed dividing the $\widehat{D}$ point estimate by 0·48, the upper and lower confidence limits by 0·42 and 0·55, respectively, based on the range of published coyote response rates (Fulmer 1990; Mitchell 2004). I compared my point estimates of $\hat{p}$ and $\widehat{D}$ to those of Hansen

(2013) using a two-sample *t*-test, and plotted variation in these parameters by ecoregion using a generalized layer acquired from The Nature Conservancy (Bailey 1997).

Results

SPreAD-GIS predictions of coyote call detectability correlated well with empirical detections in blind field trails (Cohen's W = 0·88, P < 0·01, N = 132). Using SPreAD-GIS to model site-specific call detection at 101 sites across New York State yielded $\hat{p}_s$ values ranging 0·08–0·91. Mean $\hat{p}_s$ values were not significantly different in areas where coyotes were and were not heard (t = -1·01, df = 96, P = 0·31). Call-based surveys may yield non-detection from either poor detectability or lack of a coyote vocalization altogether, so the lack of detection of animal calls in the field cannot be used to validate model predictions of animal detectability *per se*. Nevertheless, the lack of difference in $\hat{p}_s$ between the detection sites and non-detection sites indicated that our selection of sites chosen to model $\hat{p}_s$ were unbiased by differences in detectability.

Regression models relating $\hat{p}_s$ to local landscape conditions indicated that landscape properties in close proximity (1-km radius) were more strongly related to call detectability than were properties of the larger landscape (2-km radius; ΔAIC ≥ 21.9, Table 2.1). Models including the effects of forest cover, terrain complexity, and elevation of the observer outperformed simpler models (ΔAIC ≥ 14·09, Table 1), and the highest-ranked model (Table 2.2) explained a significant amount of variation (Wald χ^2 = 199, df = 7, P < 0·01; Fig. 2.2). Increasing percent forest cover predictably reduced call detectability (Table 2.2). Terrain complexity of the surrounding area had a nonlinear effect on call detectability with the greatest detectability

predicted at the lowest complexity, a rapid decline in detection as complexity increased, and a slight increase in detection indicated at the upper limit of the modeled complexity values (Fig. 2.3). Terrain complexity also interacted with elevation of the survey location such that detection increased at high elevations when terrain complexity was at either end of the range on complexity values but decreased at intermediate values (Fig. 2.3). At low elevations, detection probabilities were greatest with low terrain complexity and decreased rapidly as terrain complexity increased, similar to the relationship indicated by terrain complexity alone (Fig. 2.3). Applying the model to the landscape indicated that the highest probability of call detection occurred in the northern half of the Northern River Valleys and in scattered parts of the Hudson River Valley (Fig. 2.4). The Lake Plains region and remainder of the Northern River Valleys generally had moderate probabilities of detection whereas much of the Adirondack Park and the Alleghany Plateau had low detection rates (Fig. 2.4).

Extracting $\hat{p}_r$ values at the 541 survey locations of Hansen (2013) yielded an overall mean value for $\hat{p}_r$ (0·27, 2·7% CV) that was significantly higher and more precise than the distance sampling $\hat{p}$ (0·19, 13·5% CV, t = 2·96, df = 75, P < 0·01). Whereas the 66 coyote detections of Hansen (2013) were too few to evaluate region-specific differences in coyote detectability using distance sampling, our approach indicated large differences in coyote detectability among regions being roughly twice as high in the Lake Plains and Northern River Valleys compared to the Adirondack Mountains and Hudson River Valley (Fig. 2.5a). Using $\hat{p}_r$ to correct raw counts of coyotes from the statewide call-response surveys, we estimated a lower and more precise density of territorial pairs in the state (0·87 coyote pairs 10 km^{-2}, 95% CI: 0·64–0·94) than did distance sampling (1·3 coyote pairs 10 km^{-2}, 95% CI: 0·8–2·1; Hansen 2013).

Precision of ecoregion-specific estimates also increased compared to Hansen (2013, Fig. 2.5b), indicating a trend towards higher density populations in the Adirondack Mountains compared to the Lake Plains regions that was not apparent from the broad-scale distance sampling survey (Fig. 2.5b). Moreover, the spike in coyote detections observed in the Northern River Valleys by Hansen (2013) was likely driven in large part by the grossly higher probability of detecting coyote calls in that region rather than to a difference in coyote density (Fig. 2.5a,b).

Discussion

I demonstrated how the first principles of sound propagation can be used to meaningfully predict the probability of call detection for aural surveys of animal occurrence. The freeware SPreAD-GIS tool (Reed, Boggs & Mann 2012) combined with readily available spatial data make this process accessible for a variety of applications. My specific application to call-response surveys for a wide-ranging mammalian carnivore demonstrated several advantages over traditional distance sampling, such as finer-scale inference, reduced bias and increased precision in population estimates, and a greatly streamlined field survey effort.

Animal detectability is often heterogeneous over space and time (Bibby & Buckland 1987; Schieck 1997; Alldredge, Simons & Pollock 2007a). However, gaining sufficiently detailed information to model animal detectability with precision is difficult, especially for wide-ranging species for which detections may be too few to resolve site-specific influences. For this application, a two-stage approach to creating site-specific probabilities of detection involved modeling sound propagation for a large sample of survey locations and then predicting call detectability as a function of readily-measurable landscape covariates. Spatially-explicit

detection probabilities were on average higher and more precise than achieved via distance sampling (Hansen 2013), and consequently yielded more precise estimates of coyote density. Given sufficient survey intensity, distance sampling would theoretically be able to capture the spatial variation in call detectability (Buckland *et al.* 2001) that we modeled using SPreAD-GIS. However, intensive resampling of locations using call-response surveys may influence animal behavior (e.g. habituation to calls, avoidance of survey locations) that might undermine efforts to model spatially-explicit detectability using distance sampling (Wolfe 1974; Mitchell 2004). Moreover, estimation of distance with precision for calling animals requires some physical means of measuring distance because perceived call quality alone is insufficient (Buckland *et al.* 2001; Alldredge *et al.* 2008). Three observers triangulating on calling animals (see Hansen 2013), although useful, is a large expense in terms of time and labor that is likely prohibitive for routine population monitoring. Removing the need to estimate distance by creating a standalone detection model may therefore greatly extend the utility of call-based surveys for population monitoring by reducing the necessary field effort while also increasing the spatial resolution of population inferences.

The model reported herein will generally be applicable to future coyote surveys in New York State provided the standardized protocols and timing of the Hansen (2013) surveys are replicated. The climate conditions during other seasons, like winter, will exert different influences on sound propagation and our entire modeling process should be repeated to create a standalone model specific to the season. Even for summer-based coyote surveys, it is important to note that the statewide detectability model I produced has not been fully vetted with controlled field tests. Whereas I tested whether SPreAD-GIS would reliably propagate the

sound of a coyote call from a single point to an observer, I was unable to validate the broad-scale predictions of coyote call detectability across heterogeneous New York State. A field approach similar to the blind trails conducted herein (Fig. 2.1a) should be replicated across a range of predicted detectability values before wholesale adoption of our standalone model. Likewise, extrapolation of our model to neighboring regions should be validated for local conditions.

With respect to other species and systems, the key limitation of the soundshed approach may be availability of land cover and elevation data at a suitable resolution. Readily available landscape data from the U.S. Geological Survey and other national or international sources may be most useful for long-distance vocalizers such as mid- to large-bodied terrestrial mammals (McCarley 1975; Mitani & Stuht 1998; McComb *et al.* 2003), marine mammals, and perhaps some avian species (Morton 1975; Mack, Jones & Nelson 2003). However, aural surveys are most commonly used for songbirds, whose high frequency calls attenuate quickly over space and are generally detectable only within ~100–300 m (Morton 1975; Wolf, Howe & Davis 1995; Alldredge, Simons & Pollock 2007b). Although my modeling approach is equally applicable to short-range vocalizations its utility will obviously be limited by the resolution of available spatial data. However, should sufficient spatial and weather data be available, an interesting potential application of sound propagation modeling is correcting historical surveys to better track changes in populations over time.

As evidenced here, acoustic density estimation is a rapidly evolving area of research (Marques *et al.* 2012) and has already provided unique solutions to some of the most daunting logistical and ecological challenges facing population surveys today. Passive acoustic

monitoring has given us a window into the population biology of cetaceans (Marques *et al.* 2009; Kusel *et al.* 2011), elephants (Payne, Thompson & Kramer 2003; Thompson *et al.* 2009; Thompson, Schwager & Payne 2010), and avian species (Dawson & Efford 2009) that are otherwise challenging to monitor. SPreAD-GIS provides an invaluable tool for modeling soundsheds. Although the original application was modeling propagation of noise from a point into surrounding areas, I demonstrate its utility for modeling propagation of sound from many possible points to a central observer. Biologists have thus far used data from real-time field observers, microphone array installations, and hydrophones to build pictures of detection probabilities for calls for use with distance sampling , CMR, and SECR frameworks. My GIS-based approach is yet one more way to look at acoustic detectability, one that is adaptable to many taxa and systems. Moreover, removing the need to estimate distance altogether in aural surveys has the potential to open surveys up to citizen science applications because having a standalone correction model requires an observer merely to recognize the call of the target species and, if needed, evaluate the number of calling animals.

Table 2.1. Beta logistic regression models for predicting the probability of detecting a coyote response at a given location (n = 101). Top models are shown with number of estimable parameters (K), model log-likelihood (LL), change in Akaike's Information Criterion (Δ AIC), and model weight (ω_i).

Rank	Model components	K	LL	Δ AIC	ω_i
1	Forest-1k[1], Terr-1k[2], TerrSq-1k[3], Elev[4], Terr-1kxElev[5], Reg-LP[6], Terr-1kxReg-LP[7]	9	93·5	0·0	0·77
2	Forest-1k[1], Terr-1k[2], TerrSq-1k[3], Elev[4], Terr-1kxElev[5], Reg-LP[6]	8	91·3	2·5	0·22
3	Forest-1k[1], Terr-1k[2], TerrSq-1k[3], Elev[4], Terr-1kxElev[5]	7	87·2	8·6	0·01
4	Forest-2k[8], Terr-2k[9], TerrSq-2k[10], Elev[4], Terr-2kxElev[11], Reg-LP[6], Terr-2kxReg-LP[12]	9	82·6	21·9	0·00
5	Forest-1k[1], Terr-1k[2], TerrSq-1k[3], Elev[4], Reg-LP[6]	7	74·8	33·4	0·00
6	Forest-1k[1], Terr-1k[2], TerrSq-1k[3], Elev[4]	6	73·2	34·6	0·00
7	Forest-1k[1], Terr-1k[2], TerrSq-1k[3]	5	66·1	46·8	0·00
8	Forest-2k[8], Terr-2k[9], TerrSq-2k[10], Elev[4]	6	66·1	48·9	0·00
9	Forest-1k[1], Terr-1k[2], Elev[4]	5	64·2	50·5	0·00
10	Forest-1k[1], Terr-1k[2]	4	56·1	64·7	0·00
11	Terr-1k[2], TerrSq-1k[3]	4	51·3	74·3	0·00
12	Terr-1k[2]	3	48·2	78·7	0·00
13	Forest-2k[8]	3	47·2	80·5	0·00
14	Forest-1k[1]	3	43·4	88·1	0·00
15	Terr-2k[9]	3	41·8	91·4	0·00
16	Elev[4]	3	43·5	94·0	0·00

[1] Percent forest within 1 km of survey point.

[2] Terrain complexity represented by the coefficient of variation of elevation within 1 km of survey point.

[3] Terr-1k squared.

[4] Elevation (in meters) at survey point.

[5] Interaction term between Terr-1k and Elev.

[6] Ecoregional variable specifying the Lake Plains ecoregion.

[7] Interaction term between Terr-1k and Reg-LP.

[8] Percent forest within 2 km of survey point.

[9] Terrain complexity represented by the coefficient of variation of elevation within 2 km of survey point.

[10] Terr-2k squared.

[11] Interaction term between Terr-2k and Elev.

[12] Interaction term between Terr-2k and Reg-LP.

Table 2.2. Highest-ranked beta logistic regression model for predicting the probability of detecting a coyote response ($\hat{p}_s$) in New York State.

Model variables	β	SE	*z*	*P*
Landscape variables				
Forest (% within 1 km of survey point)	-1·7	0·3	-6·1	≤ 0·01
Terrain complexity (%CV of elevation within 1 km of survey point)	-59·1	6·5	-9·1	≤ 0·01
Terrain complexity squared	181·7	26·7	6·8	≤ 0·01
Observer elevation at survey point (meters/1,000)	-4·9	0·6	-7·8	≤ 0·01
Lake Plains ecoregion	-0·9	0·3	-3·5	≤ 0·01
Interaction terms				
Terrain complexity x observer elevation	72·4	11·3	6·4	≤ 0·01
Terrain complexity x ecoregion	11·6	5·3	2·2	0·03
Constant	2.8	0·3	9·3	≤ 0·01

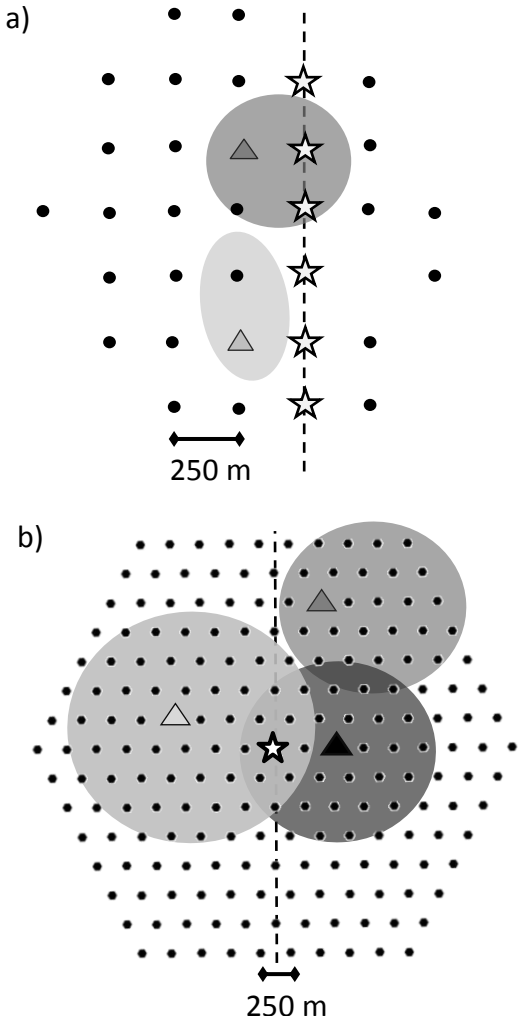

Figure 2.1. Layout of points used for SPreAD-GIS coyote aural detection model validation and application. (a) Empirical tests of coyote calls emitted from 28 locations (black circles) and listened for by 6 roadside observers (stars). Shaded regions indicate hypothetical SPreAD-GIS results for two locations (triangles), indicating that a call from the dark gray location but not the light gray location should be detectable by observers. (b) Estimation of site-specific probability of detection was based on sound propagation from 198 uniformly placed locations (black circles) to a central observation point (star). Sound-sheds that overlapped the observer (e.g. two out of the three shaded areas shown) were counted as detections.

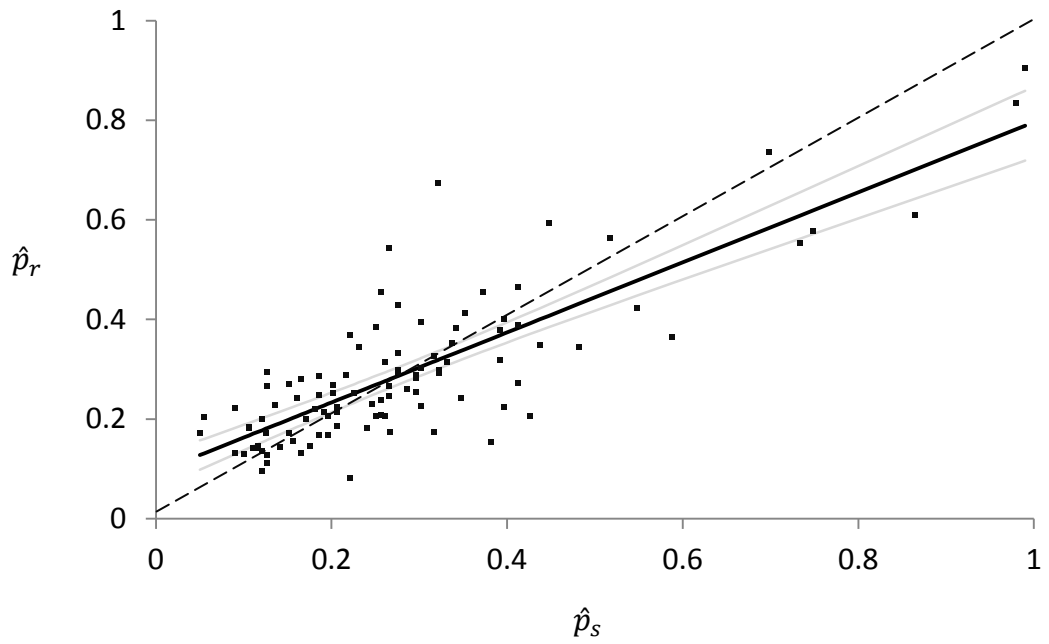

Figure 2.2. Correlation (with 95% prediction intervals) between SPreAD-GIS modeled detectability, $\hat{p}_s$, and beta-logistic model predictions, $\hat{p}_r$ with a 1:1 correlation (dashed line) for comparison.

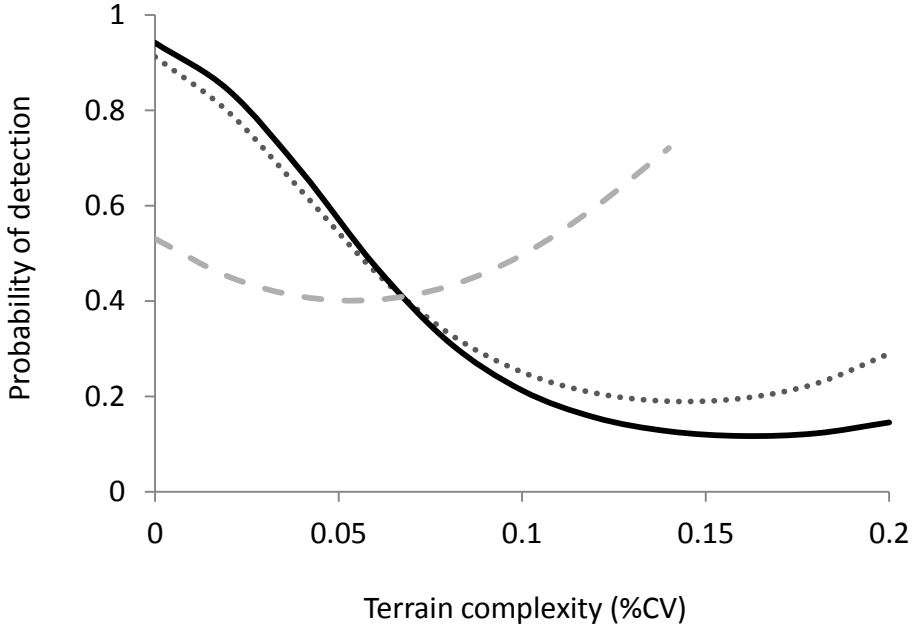

Figure 2.3. Partial slopes showing effects of terrain complexity alone (solid black line) and the interaction between terrain complexity and observer elevation on probability of detecting a coyote call, $\hat{p}_r$, given low elevation (90 m, gray dotted line) and high elevation (547 m, gray dashed line).

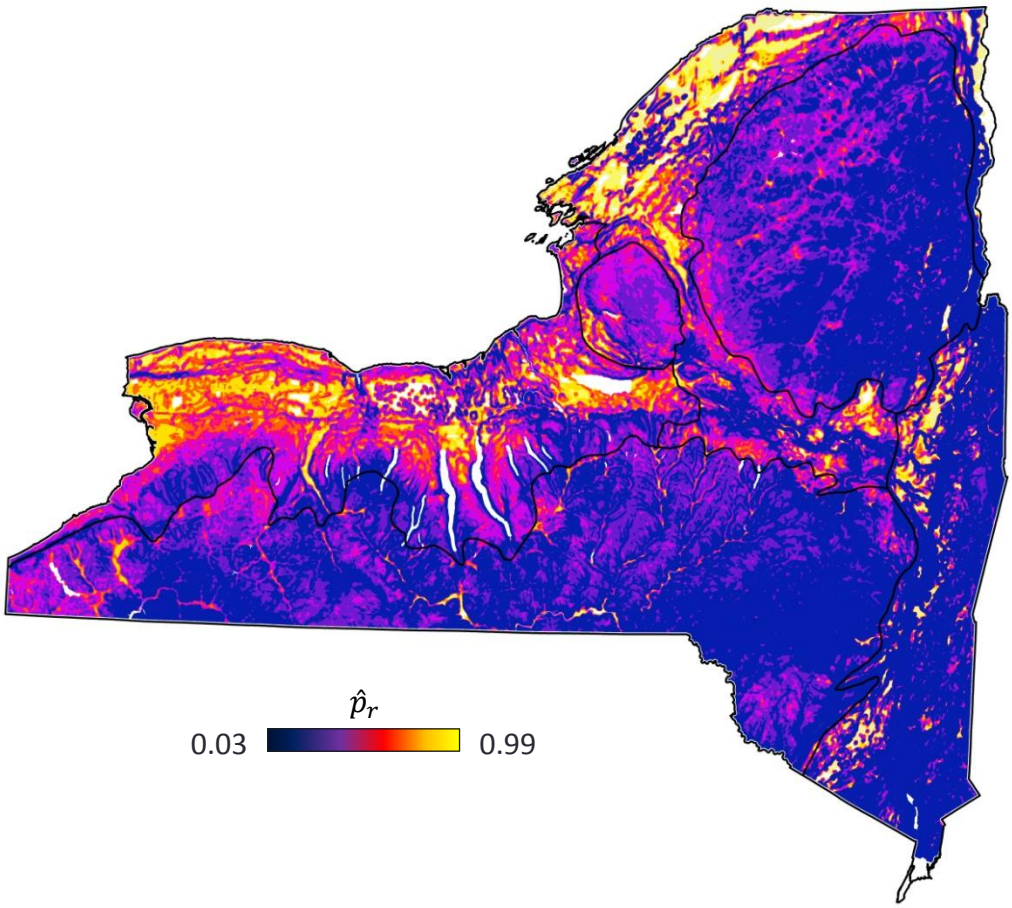

Figure 2.4. Predicted probability of detecting a calling coyote, $\hat{p}_r$, in New York State and generalized ecoregions (LP = Lake Plains, AP = Allegheny Plateau, NRV = Northern River Valleys, ADK = Adirondack Mountains, HRV = Hudson River Valley) based on a beta logistic regression of sound propagation models and landscape characteristics.

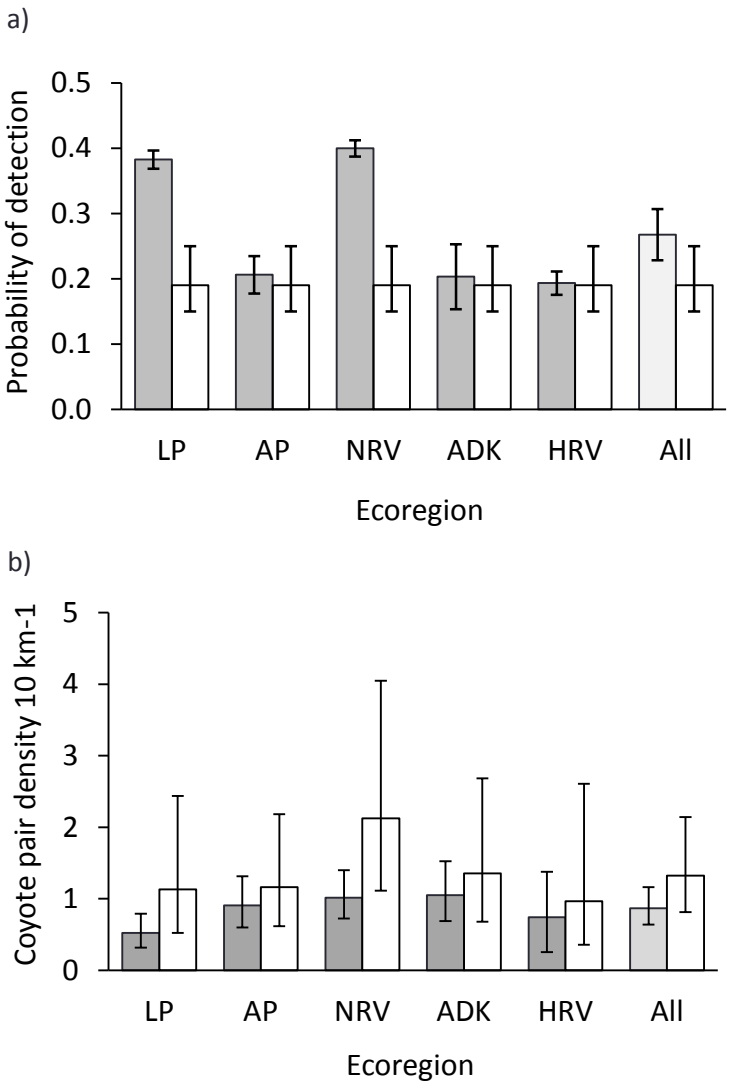

Figure 2.5. (a) Mean probability of detecting a coyote call (with 95% confidence intervals) within generalized ecoregions and overall (LP = Lake Plains, AP = Allegheny Plateau, NRV = Northern River Valleys, ADK = Adirondack Mountains, HRV = Hudson River Valley, and All = Statewide average). (b) Estimates of coyote pair density (with 95% confidence intervals) within ecoregions and overall. Shown separately for the standalone detectability model produced herein (gray) and the distance sampling (white) effort of Hansen (2013).

Conclusions

My research demonstrated two approaches in which call-response surveys can be successfully used to estimate large-scale yet precise measures of true abundance that accounts for animals missed during a survey. Chapter 1 investigated the efficacy of call-response surveys within a distance sampling framework to estimate density of vocalizing animals. The approach requires careful consideration of key assumptions and identification of a precise method for distance estimation to be effective. Chapter 2 explored sound propagation models as a means to predict a site-specific probability of call detection for vocal animals, an approach that needs only commonly available spatial data and a single field observer. Both methods produced comparable estimates for a single population but each has unique strengths and weaknesses that will affect how they are best implemented in a given situation.

Perhaps the greatest strength of this study was the opportunity to independently apply two unique approaches to the same problem of detection probability estimation. The final abundance estimates provided by distance sampling ($\widehat{N}$ = 14,310 coyote pairs, 95% CI: 8,719–22,887) and my spatially explicit approach ($\widehat{N}$ = 9,482 coyote pairs, 95% CI: 6,975–10,245) indicate that the later method provided a more precise estimate given the available data. That the probability of detection estimated via distance sampling was significantly different from that of the GIS-based approach does not necessarily mean that distance sampling is not a viable option, it simply requires more field intensive effort and care that attendant assumptions are fully met. With sufficient data to estimate a second detection function and better represent variation in detection across the state (as indicated by my GIS-based estimates), the differences in ecoregional and overall density between the two approaches would have been largely

accounted for. Future monitoring of coyote populations in New York would be most efficient and cost effective utilizing the spatially explicit standalone approach but further refinement is still possible. To apply the method to its greatest advantage I recommend that more intensive efforts be made to field validate the site-specific probability of detection process across a more diverse set of localized landscape conditions than was possible during this study.

The above issues notwithstanding, my research is a novel addition to the body of work exploring new frontiers in acoustic density estimation. Both approaches are highly adaptable to varying systems and can be applied to frameworks meant to provide estimates of true abundance or, at the very least, repeatable corrected estimates of relative abundance appropriate for identifying population changes over time. These novel approaches have shown that aurally-based population estimation techniques can indeed be precise and scalable, providing efficient and cost effective means for gaining valuable population information.

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Appendices

Appendix I: List of estimated ambient noise SPL values by cover type used to calculate excess noise levels in sound propagation models at 1 KHz, Chapter 2.

Cover type	Ambient noise (dB)
Evergreen	19
Grassland	20
Deciduous	18
Shrub	22
Urban	19
Open water	24

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