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Research Article

Estimating Abundance of Sitka Black-Tailed Deer Using DNA From Fecal Pellets

TODD J. BRINKMAN,[1] *Institute of Arctic Biology and Department of Biology and Wildlife, University of Alaska Fairbanks, Fairbanks, AK 99775, USA*

DAVID K. PERSON, *Alaska Department of Fish and Game, Division of Wildlife Conservation, Ketchikan, AK 99901, USA*

F. STUART CHAPIN, III, *Institute of Arctic Biology and Department of Biology and Wildlife, University of Alaska Fairbanks, Fairbanks, AK 99775, USA*

WINSTON SMITH, *USDA Forest Service, Pacific Northwest Research Station, Forestry Sciences Laboratory, Olympia, WA 98512, USA*

KRIS J. HUNDERTMARK, *Institute of Arctic Biology and Department of Biology and Wildlife, University of Alaska Fairbanks, Fairbanks, AK 99775, USA*

ABSTRACT Densely vegetated environments have hindered collection of basic population parameters on forest-dwelling ungulates. Our objective was to develop a mark–recapture technique that used DNA from fecal pellets to overcome constraints associated with estimating abundance of ungulates in landscapes where direct observation is difficult. We tested our technique on Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) in the temperate coastal rainforest of Southeast Alaska. During 2006–2008, we sampled fecal pellets of deer along trail transects in 3 intensively logged watersheds on Prince of Wales Island, Alaska. We extracted DNA from the surface of fecal pellets and used microsatellite markers to identify individual deer. With genotypes of individual deer, we estimated abundance of deer with moderate precision (±20%) using mark–recapture models. Combining all study sites, we identified a 30% (SE = 5.1%) decline in abundance during our 3-year study, which we attributed to 3 consecutive severe winters. We determined that deer densities in managed land logged >30 years ago (7 deer/km^2, SE = 1.3) supported fewer deer compared to both managed land logged <30 years ago (10 deer/km^2, SE = 1.5) and unmanaged land (12 deer/km^2, SE = 1.4). Our study provides the first estimates of abundance (based on individually identified deer) for Sitka black-tailed deer and the first estimates of abundance of an unenclosed ungulate population using DNA from fecal pellets. Our tool enables managers to accurately and precisely estimate the abundance of deer in densely vegetated habitats using a non-invasive approach. © 2011 The Wildlife Society.

KEY WORDS abundance, Alaska, density, DNA, fecal pellets, forest, logging, mark–recapture, *Odocoileus hemionus sitkensis*, Sitka black-tailed deer.

From Africa to Alaska, densely vegetated environments have hindered the ability of wildlife biologists to estimate and monitor populations of forest-dwelling ungulates (Ratcliffe 1987, Koster and Hart 1988, van Vliet et al. 2008). Direct counts from aerial surveys are seldom feasible because many animals are hidden under forest canopies that cannot be penetrated even with infrared sensors and other advanced remote-sensing technologies. Ground surveys such as roadside or spotlight counts also are frequently unreliable because animals are difficult to detect in forested habitat, and thus surveys often are limited to easily accessible roads or trails. Live-capture and photographic mark–recapture methods usually are very expensive and limited in spatial scope. Those techniques rarely yield sample sizes sufficient to extrapolate to population and landscape scales. Consequently, population indices derived from fecal pellet counts have become widely used to monitor ungulate populations in forested landscapes (Neff 1968, Putman 1984, Kirchhoff and Pitcher 1988, Forsyth et al. 2007, van Vliet et al. 2008) and are sometimes employed to monitor trends at large regional scales (Kirchhoff and Pitcher 1988, Patterson and Power 2002). However, fecal counts are confounded by seasonal and weather-related variability that influences persistence of pellets in the environment, defecation rates, and detectability of pellets in different habitats. Moreover, in many circumstances, procedures to convert pellet counts to numbers of deer are based on few empirical data and rarely evaluated over time. As a result, population estimates based on pellet counts can be imprecise, inaccurate, and often unreliable (Fuller 1991, Campbell et al. 2004, Smart et al. 2004).

During the last 2 decades, genetic techniques for extracting DNA from hair or feces were developed with applications for estimating abundance (i.e., no. of animals) in forested landscapes (Bellemain et al. 2005, Waits and Paetkau 2005, Ulizio et al. 2006, Pauli et al. 2008, Schwartz and Monfort 2008). Non-invasive genetic methods commonly are used to monitor forest carnivores (Ernest et al. 2000, Boulanger et al. 2004, Hedmark et al. 2004, Kendall et al. 2008, Williams et al. 2009); however, similar efforts to apply genetic methods to free-ranging ungulates are rare (Belant et al. 2007, Van Vliet et al. 2008, Gebremedhin et al. 2009). Belant et al. (2007) identified individual white-tailed deer (*Odocoileus virginianus*) using DNA from hair, and Valière et al. (2007) estimated population size of an enclosed population of red deer (*Cervus elaphus*) using fecal DNA. Nonetheless, no study has successfully estimated abundance of an unenclosed ungulate population using fecal DNA.

Abundance and relative ease of collection are attractive properties of using pellets for DNA extraction, particularly at landscape scales. The opportunities and pitfalls of using

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[1]*E-mail: tjbrinkman@alaska.edu*

DNA from feces or hair of ungulates to genotype individuals, a necessary prerequisite of mark–recapture techniques, are described by several authors (Maudet et al. 2004, Ball et al. 2007, Valière et al. 2007). Problems associated with fecal DNA include contamination by microorganisms or digested food items, sensitivity to weather, high polymerase chain reaction (PCR)-inhibitor to DNA ratios, and high amplification and genotyping errors (Maudet et al. 2004, Buchan et al. 2005, Murphy et al. 2007, Brinkman et al. 2009*a*). Wet weather conditions also contribute to high rates of error in DNA analyzed from pellets because the genetic material is degraded by water, washed off the pellets, or pellets fully dissolve (Brinkman et al. 2009*a*). In addition, the number of pellets deposited by deer (Fisch 1979, Harestad and Bunnell 1987) can swamp the processing capacity of genetic laboratories requiring carefully designed sampling criteria to reduce the number of pellets collected without introducing sampling bias.

Taking into consideration these concerns, we developed and tested a protocol to efficiently estimate abundance of Sitka black-tailed deer (*O. hemionus sitkensis*), a forest-dwelling ungulate in Southeast Alaska, using DNA extracted from naturally deposited fecal pellets. Sitka black-tailed deer inhabit dense temperate rainforest and are difficult to enumerate. State and federal wildlife managers rely on counts of fecal pellet groups to monitor population trends of deer (Kirchhoff and Pitcher 1988). However, those data only provide crude indices of trends and suffer from other confounding factors described above. Several circumstances underscore the need for reliable estimates of deer population size in Southeast Alaska. Fifty years of industrial-scale logging significantly altered landscapes by converting old-growth forest stands into clearcuts and second-growth forests (Alaback 1982). Those changes presumably will cause a long-term decline in deer populations and make them more vulnerable to winter weather conditions (Wallmo and Schoen 1980, Schoen et al. 1988, Parker et al. 1999). In Alaska and elsewhere, there are few reliable quantitative data concerning changes in deer abundance following timber harvest. Also, without accurate and precise methods to monitor populations it is difficult to evaluate the impact on deer of changes in patterns of hunting. Although studies were conducted to better understand the response of hunters to forest changes caused by logging (Brinkman et al. 2009*b*), hunter concerns about those changes cannot be effectively addressed without information on deer population trends (Unit 2 Deer Planning Subcommittee 2005).

We sought a method to estimate abundance of deer that was reliable, flexible to local environmental conditions, and useful at multiple temporal and spatial scales. We had to develop a pellet sampling design that maximized encounter rates with fecal pellets and simultaneously minimized the degrading effects of wet weather on the epithelial cell DNA adhering to pellets. We also had to adapt accepted methods of mark–recapture analyses to our sampling design and genetic data. To demonstrate the utility of our method, we estimated population abundance of deer over 3 years within 3 study sites extensively altered by commercial logging. During those 3 years, our study sites experienced 3 winters (2 severe) with above average snowfall affording us an opportunity to test our method during a period when the deer population was expected to decline and to examine how management (i.e., logging) may have influenced deer population response to climatic severity. The rapid ecological changes in our study area are representative of those experienced globally. Therefore, the setting in which we tested the performance of our DNA-based technique should provide a useful example of the application potential to a broad audience.

STUDY AREA

We conducted our research on Prince of Wales Island, Alaska (approx. 55°00′00″N–136°00′00″W; Fig. 1). Most of the island was within the Tongass National Forest, which was administered by the United States Department of Agriculture (USDA) Forest Service. Topography included rugged mountains extending to 1,160 m in elevation with habitats at <600 m dominated by temperate coniferous rainforest consisting primarily of Sitka spruce (*Picea sitchensis*) and western hemlock (*Tsuga heterophylla*; Alaback 1982). Annual precipitation varied from 130 cm to 400 cm, and mean monthly temperatures ranged from 1°C in January to 13°C in July. Between winters 1948 and 2008, mean annual snowfall at sea level was 115 cm (SE = 9.5) at Annette Island, the closest weather station (Alaska Climate Research Center 2009). Snowfall was above the 60-year mean for southern Southeast Alaska in all sites during our study period (2006–2008). Reported snowfall was 128, 187, and 161 cm for 2006, 2007, and 2008, respectively (Annette Island weather station, Alaska Climate Research Center 2009). Within each study site, habitat ranged from 0 m to 1,000 m in elevation. Snowfall, snow depth, and persistence increased with elevation.

We established study sites in the Maybeso Creek (Maybeso, 35 km^2), upper Staney Creek (Staney, 43 km^2), and upper Steelhead Creek (Steelhead, 33 km^2) watersheds located within the north-central portion of Prince of Wales Island (Fig. 1). All study sites were accessible by roads maintained for passenger–vehicle use during snow-free months. Each study site encompassed a mosaic of productive old-growth forest, unproductive old-growth forests on hydric soils, clearcuts at various successional stages including stem-exclusion forest and open muskeg heaths. Each watershed was bounded by alpine habitat and rugged mountains not occupied by deer during our annual study period because snow depths forced deer to remain below approximately 300 m in elevation. Old-growth forest consisted of uneven-aged stands of large and old conifers undisturbed by logging. The forest canopy was dense but with many openings and patches of thick understory vegetation consisting of blueberry and huckleberry shrubs (*Vaccinium* spp.), Devil's club (*Oplopanax horridus*), and skunk cabbage (*Lysichiton americanum*; Pojar 1994). Alpine tundra was treeless habitat usually above 800 m dominated by low-growing plants adapted to snow pack and wind abrasion; alpine tundra habitat was occupied by migrating deer during snow-free months (Schoen and Kirchhoff 1990). Muskeg

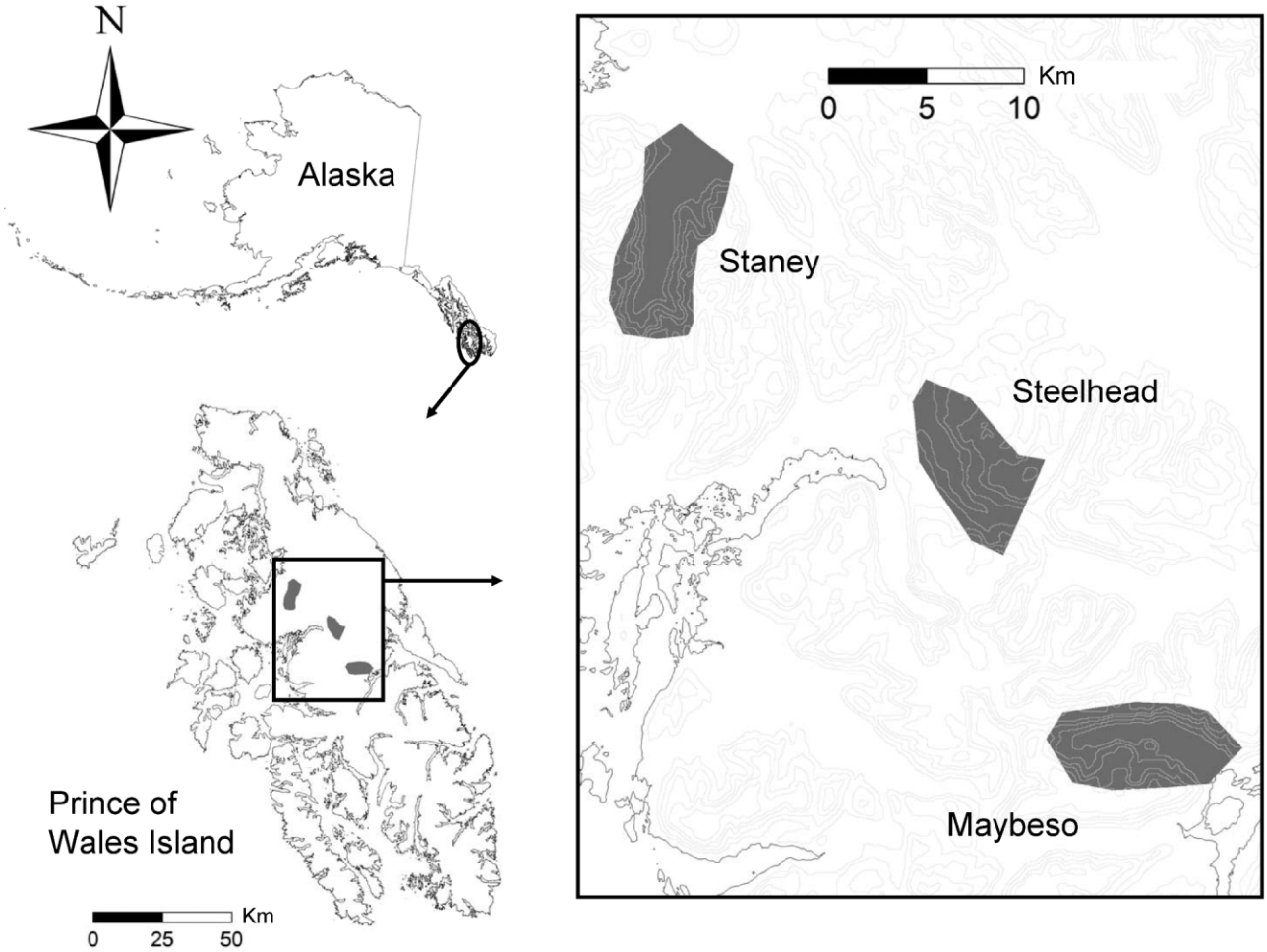

Figure 1. Location of study sites on Prince of Wales Island, Alaska, where we conducted research on Sitka black-tailed deer during 2006–2008.

(peatlands or heath) communities were poorly drained and sparsely forested areas dominated by ground cover of sphagnum mosses (*Sphagnum* spp.) and sedges (*Carex* spp.; USDA 2007). Clearcuts were habitats in which all overstory trees were removed by timber harvest. Natural conifer regeneration occurred within 5 years of logging and clearcuts <10 years old typically contained sapling-stage conifers and thick growth of shrubs (e.g., *Vaccinium* spp.), and herbaceous plants. After 10 years, the conifer regeneration was usually >2 m high (pole stage) and surrounded by dense understory vegetation. Clearcuts transitioned into stem-exclusion forests at about 25–30 years after harvest. Stem-exclusion forests were thick, even-aged stands of trees with depauperate understory vegetation (Alaback 1982). Precommercially thinned forest consisted of sapling and pole-stage clearcuts that were thinned approximately 10–20 years after being logged (Deal and Farr 1994). Thinned stands had sparse canopies that tended to delay their transition into stem-exclusion forest by 10–15 years. However, they also contained abundant slash from the thinning process, which may have hindered movements of deer through the habitat (Farmer et al. 2006).

We can group habitat types in our study sites into 2 general categories: managed and unmanaged land. Managed (i.e., logged) land included clearcut, stem-exclusion, and thinned stands. Unmanaged land included old-growth forests and muskeg habitat. In Maybeso, all managed stands were logged >30 years before the study and were stem-exclusion forests. In Staney and Steelhead, managed stands were logged <30 years ago, and we consider them clearcut forest. Although, we combined various habitat types, canopy cover, and biomass of deer forage varies among habitat types within managed and unmanaged land (Hanley and McKendrick 1983, Parker et al. 1999). Also, risk of mortality among individual deer varies among habitat types within managed and unmanaged land (Farmer et al. 2006). However, our sampling design and sample size did not allow estimates of abundance in habitat types (e.g., muskeg) within each general category of land.

Sitka black-tailed deer are the most widely distributed and abundant ungulates in Southeast Alaska. They are principal prey of wolves (*Canis lupus*), important prey of black bears (*Ursus americanus*) and brown bears (*U. arctos*), and are the primary source of red meat for subsistence hunters in Southeast Alaska (Kruse and Frazier 1988, Hanley 1993, Mazza 2003). Other mammals within the study areas included marten (*Martes americana*), beaver (*Castor canadensis*), and several species of rodents.

METHODS

From the beginning of snow melt (about 15 Mar) until appearance of leaves occurred (about 15 May) during 2006–2008, we sampled deer fecal pellets from 31 belt transects (Maybeso = 6, Staney = 16, Steelhead = 9), covering an area of 13,372 m^2, 17,796 m^2, and 9,970 m^2 in Maybeso, Staney, and Steelhead study sites, respectively. We established transects to follow deer trails. In our study sites, Brinkman (2009) reported that encounter rates with fecal pellet groups of deer were greater along deer trails compared to straight-line transects. To determine this, Brinkman (2009) established 6–8 100 m^2 plots in each of our study sites in old-growth forest to identify deer trail density and percentage of pellet groups deposited on the trail network. Brinkman (2009) estimated that deer trails (when buffered by 1 m on each side of the center of the trail) covered approximately 30% of the area within each plot, and deer deposited 67% of their pellets on the buffered trail network. Also, trail density and percentage of pellet groups deposited on the trail system was similar across watersheds (Brinkman 2009). During a subsequent field test, Brinkman (2009) surveyed overlapping (e.g., same starting point, same direction, same distance sampled) deer trail and straight-line transects and determined that encounter rates with pellet groups was 48% higher using deer trails. Because of the ubiquity and uniformity of deer trails across the landscape, we made the plausible assumption that using deer trails created the best opportunity to foster mark–recapture methods while also allowing extrapolation and comparison of estimates. We considered over and underestimation of population estimates unlikely because the uniform availability of trails provided no biological reason to expect heterogeneity of use.

After identifying the habitat type we wanted to sample, we used a random-number generator to assign a distance from habitat edge to establish the starting point of the deer trail transect. Similar to a straight-line transect or sampling grids, we had a predetermined survey direction with systematic sampling. We used a predefined bearing to increase the likelihood that we were sampling habitat types proportionally to their representation within the watershed to increase inference at a larger scale. We traveled in the direction of a predefined bearing (e.g., 45°) from the starting point until we encountered a deer trail. We would then survey that trail until we encountered another trail. If another trail intersected the trail being surveyed, we used a compass to determine which trail more closely paralleled the direction of the predefined bearing (45°) and we continued surveying along that trail. We intensively marked deer trails with fluorescent flagging to ensure repeatability within and across field seasons. Using a predetermined compass bearing to select trails to be surveyed was the fundamental aspect of our technique that minimized subjectivity of trail selection. Further, systematic selection of deer trails using compass bearings allowed an equally random opportunity to sample a range of deer trails, if varying frequencies of use existed.

As mentioned briefly, we positioned transects to ensure they traversed a proportionally representative sample of all types of deer habitat available in our study sites. For example, if 25% of the landscape in our study site was composed of managed forest, then 25% of the total area of transects in that study site traversed managed forest. Furthermore, transects traversed a variety of other landscape features (e.g., different slopes, elevations, aspects, and distances from roads). To optimize opportunities to collect pellets from different individual deer across our study sites, we separated all portions of adjacent transects by at least the radius of a home range of deer (0.78 km^2) as estimated from radiocollared deer on Prince of Wales Island (Farmer et al. 2006).

We sampled 4–6 fecal pellets from each fecal pellet group we encountered along transects. We resampled transects in Maybeso, Staney, and Steelhead a mean of 6.2 (SE = 0.27), 5.0 (SE = 0.11), and 4.1 (SE = 0.22) times (i.e., capture occasions) per annual field season, respectively. Timing of snow melt mainly determined how many times we resampled transects each year. We resampled each path transect after about 10 days to ensure that most pellets would yield usable DNA (Brinkman et al. 2009*a*). After sampling from groups, we removed all remaining pellets from the sampling area during each sampling occasion. Therefore, we assumed that all pellet groups encountered during the next sampling occasion were deposited within that 10-day period. During the first sampling occasion of the year for each transect, however, we only collected pellets from groups that appeared to be recently deposited (shiny with a mucus sheen) to avoid sampling pellets from which we were unlikely to extract useful DNA (Brinkman et al. 2010). We collected pellets from each pellet group deposited within 1 m of the center of the deer trail transect; thus, we were sampling a prescribed width of 2 m (e.g., belt transect; Seber 1982). Although we only were sampling from pellet groups within the 2-m width to ensure easy detection, we removed all pellets within a 4-m width during each sampling occasion to reduce the chance of sampling from a pellet group that was present during a previous sampling occasion. Using a handheld Global Positioning System, we recorded time and location of each pellet group from which we sampled. We collected each sample of pellets with unused and sterile latex gloves, placed samples in plastic conical tubes, filled tubes with 90% ethanol for preservation, and stored them at room temperature for 1–6 months until DNA extraction.

Following a protocol established by Brinkman et al. (2010), we extracted genomic DNA from the surface of deer fecal pellets using the DNeasy Tissue Kit (Qiagen Inc. Valencia, CA) and used 7 microsatellite markers to conduct multiplex PCR reactions using Qiagen Multiplex Master Mix® (Qiagen Inc.) according to manufacturer's instructions. We followed a rigorous genotyping protocol to prevent, mitigate, and report genotyping errors. We used a multitube approach (i.e., re-analyzed the same sample several times; Taberlet et al. 1996) to identify a consensus genotype and limit errors before statistical modeling. Because we never observed or handled deer, muscle, blood, or other tissue sample references were not available to compare with DNA extracted from fecal pellets. Our estimated probability of identity (PID) calculated using GenAlEx (Peakall and Smouse 2006) was 0.0003 (Brinkman et al. 2010). In general,

PID should be <0.001 (Schwartz and Monfort 2008). Summarized by individual marker per reaction, error rates did not exceed 5%. We re-analyzed samples 3–6 times until we identified a consensus genotype without errors. Through our rigorous genotyping protocol, we discarded 49% of samples and 77% of the 30 microsatellite markers tested to ensure accuracy. Brinkman et al. (2010) detailed the genotyping performance of those data.

To estimate population size, we used Huggins closed models (Huggins 1991) in Program MARK (White and Burnham 1999, White 2008). We developed encounter histories tabulated for all sampling occasions during an annual sampling season for each deer in each study area. Initially, we experimented with open robust design models (Kendall and Bjorkland 2001), but survival and emigration probability parameters were not estimable (they all had unrealistic SE or 95% CI), potentially creating biased abundance estimates. To foster a less cumbersome set of parameters and to allow the opportunity for a more constrained model to test our technique, we did not consider closed models incorporating mixtures and genotyping error (i.e., misidentification; Pledger 2000, Lukacs and Burnham 2005). We lacked a plausible biological mechanism to support the expectation that individual deer had intrinsically different capture probabilities that would warrant investigation of mixture models. Further, our genotype data underwent extensive quality control prior to inclusion into models (Brinkman et al. 2010). We excluded individual loci and samples with high error rates from our dataset before modeling.

Our assumption of closure was reasonable because during our sampling period (15 Mar–15 May) deer were not migrating, dispersing, fawning, or being legally harvested by hunters. Sitka black-tailed deer also show high-site fidelity while occupying seasonal ranges (Farmer et al. 2006). Some deer may have been killed by predators (i.e., wolves, illegal hunting) and factors related to winter weather; however, we assumed that these variables were not significant during our sampling periods and did not warrant using open-population models instead of closed models for estimating abundance. We evaluated our assumption of population closure using Program CloseTest, which tests the null hypothesis of a closed population model with time variation against the open-population Jolly-Seber model as a specific alternative (Stanley and Burnham 1999). We tested ($\alpha = 0.05$) all sites and years independently ($n = 9$) for closure.

We entered year and habitat (whether we captured a deer within managed or unmanaged land) within each study site as group covariates, which created 18 groups (2 habitat types × 3 years × 3 study sites). We derived estimates of population size for each year, within each study site, and within 2 habitat types (i.e., managed and unmanaged land). Therefore, we constructed models to derive 18 estimates of abundance assuming closure within years and within study sites but not across study sites and across years. Because sampling areas within an individual study site did not contain both clearcuts and stem-exclusion forest, the addition of one habitat covariate allowed us to model differences among unmanaged land and between both types of managed land. For example, including the habitat covariate in a row of the design matrix that corresponded to capture histories in Maybeso allowed us to incorporate differences in unmanaged and stem-exclusion forest. Similarly, adding the individual covariate to rows corresponding to Staney or Steelhead study sites allowed us to incorporate differences between clearcuts and unmanaged land.

We constructed biologically plausible models a priori, which allowed varying capture probabilities during sampling. Those models included time (sampling occasion) variation (*time*), linear-trend time variation (*Time linear*), varying capture probability during first capture occasion (*time1*), and a habitat covariate that represented capture histories for deer located in managed or unmanaged land. We included time variation to incorporate differences in capture probabilities between sampling occasions within years. We included linear-trend time variation to incorporate a potential increase in capture probability with each subsequent capture occasion within years. Because we sampled during late winter and early spring, during which forage intake of deer may increase with greening and growth of vegetation, we hypothesized that capture opportunities would increase because pellet deposition would increase. We incorporated differences in capture probability during first capture occasion because we predicted that over-winter deposition and persistence of pellet groups on sampling transects may inflate captures during our first sampling occasion. We assumed that behavioral response of deer to our sampling scheme was minimal because we were using a non-invasive approach that resulted in no direct disturbance to deer and minimal indirect disturbance to deer from our presence on path transects every 10 days.

We used Akaike's Information Criterion (AIC_c, adjusted for sample size) and AIC_c weights to determine the best approximating model among the suite of candidate models. That approach determines the model that best explains the data while incorporating the fewest parameters and thus balances tradeoffs between sampling variance and bias (Burnham and Anderson 2002). We used the difference between AIC_c values from our alternative models as the basis of comparison. Within Program MARK, we used AIC_c weights to derive averaged population estimates (with unconditional variance; Buckland et al. 1997) to further account for model selection uncertainty (Burnham and Anderson 2002).

In general, conversion of abundance estimates to density estimates may be biased due to boundary effects that vary with transect layout and home range size (Efford et al. 2004). Locations of our sampling transects did not allow us to calculate density using maximum likelihood or inverse prediction methods (Program DENSITY, Version 4.3.2, http://www.otago.ac.nz/density accessed 5 May 2009; Efford et al. 2004). We placed our sampling transects irregularly within study sites with regards to spacing and density to allow representative sampling of all habitat types. We were able to incorporate our spatially explicit capture and

recapture location data using measurements of the maximum mean distance between successive captures (i.e., recapture locations of the same deer) of an individual because nearly all transects were longer than this value. We quantified our effective sampling area (i.e., spatial extent of the estimated population; $\hat{A}$) by estimating the full mean maximum recapture distance (MMRD) of genotyped individuals and then assigning a strip boundary around each transect using that value. Using MMRD is one of several conventional approaches for establishing $\hat{A}$ (Otis et al. 1978, Efford et al. 2004). Parmenter et al. (2003) found MMRD to be the most accurate method to delineate the area over which abundance was estimated for several species of mammals.

We estimated density ($\hat{D}$) by dividing our abundance estimate ($\hat{N}$) by $\hat{A}$ (i.e., $\hat{D} = \hat{N}/\hat{A}$). We calculated area of managed and unmanaged land in $\hat{A}$ around each transects. We used the delta method to calculate variance of our density estimates (Wilson and Anderson 1985).

We used Geographic Information System (GIS) programs ArcView 3.3, ArcMap 9.0, and Hawth's Analysis Tools in ArcMap 9.0 (Beyer 2007) to quantify forest habitat composition in relation to transect, individual deer location as assigned from fecal DNA, and deer density and abundance estimates. Geographic Information System geodatabases and shapefiles of landcover types and logging activity used in analyses were initially created by the USDA Forest Service. Metadata for spatial data layers we used were available at the Southeast Alaska GIS Library (2010). We calculated descriptive statistics not included in output files of Programs MARK and DENSITY using computer program SPSS (SPSS Inc., Chicago, IL). Because null hypothesis tests of significance and associated *P*-values should not be mixed with results from an information-theoretic approach (e.g., AIC_c; Anderson and Burnham 2002, Burnham and Anderson 2002), we did not test for significant differences in abundance and density estimates among study sites and years or between forest habitat types (managed vs. unmanaged). Instead, we reported absolute values. We considered deer abundance and density to have changed among years if 95% confidence intervals around estimates did not overlap. We conducted nonparametric chi-squared tests to determine differences in MMRD among individual deer, study sites, and years.

RESULTS

We included 2,248 fecal pellet samples for DNA analysis, successfully genotyped 1,156 (51%) samples, and identified 737 deer (Table 1). We often recaptured the same deer during succeeding years; however, we assigned those deer unique identifications within each year because we calculated estimates annually. Our genotyping success during 2008 (87%) was double that of 2006 (44%) and 2007 (45%).

We did not identify a violation of population closure during our sampling periods. Based on AIC_c weight, we obtained 5 plausible models (Table 2). All supported models allowed capture probabilities to vary by time with each sampling occasion, and 4 models incorporated differences in capture probability between managed and unmanaged land. Although we used model averaging to estimate abundance, 2 models shared >50% weight and fit the data best: 1) the model that allowed capture probability to vary with time (i.e., each sampling occasion) and in clearcut forest and 2) the model that allowed capture probability to vary with time and in stem-exclusion forest and clearcut forest. Combining years, study sites, and habitat types, we estimated that mean capture probability of deer was 0.14 (SE = 0.014) per sampling occasion and ranged from 0.05 (SE = 0.011) to 0.19 (SE = 0.016; Fig. 2). Our data were not supported by models incorporating differences in capture probability during the first sampling occasion or models incorporating a linear-trend in capture probability over time. Those models had AIC_c weights $<1.0 \times 10^{-5}$.

Analyzing habitat type separately within sites, our estimates of abundance declined in unmanaged land by 62% (SE = 8.5%) in Maybeso. Considering 95% confidence intervals, Staney ($\Delta = -21\%$, SE = 10.5%) and Steelhead ($\Delta = -13\%$, SE = 12.6%) estimates of abundance did not change from 2006 to 2008 (Table 1). In managed land, abundance in Maybeso (stem-exclusion forest, $\Delta = +23\%$, SE = 27.8%), Staney (clearcut forest, $\Delta = -27\%$,

Table 1. Number of individuals genotyped and model-averaged estimates of abundance (SE) for Sitka black-tailed deer in each study site during 2006–2008 in managed, unmanaged, and all habitat types on Prince of Wales Island, Alaska.

	Maybeso			Staney			Steelhead		
	2006	2007	2008	2006	2007	2008	2006	2007	2008
Unmanaged land									
Genotyped	87	51	33	73	65	58	47	38	41
Abundance	127	74	48	107	95	84	69	54	60
SE	9.5	6.7	5.2	8.5	7.8	7.3	6.4	5.5	5.9
Managed land									
Genotyped	17[a]	31[a]	21[a]	54[b]	46[b]	39[b]	14[b]	10[b]	12[b]
Abundance	26[a]	46[a]	32[a]	73[b]	62[b]	53[b]	19[b]	14[b]	18[b]
SE	4.7	7.1	5.5	7.0	6.2	5.5	2.9	2.4	2.7
Total									
Genotyped	104	82	54	127	111	97	61	48	53
Abundance	153	120	80	180	157	137	88	68	78
SE	10.6	9.8	7.6	11.0	10.0	9.1	7.0	6.0	6.5

[a] Managed land was stem-exclusion forest (logged >30 years ago) in the Maybeso study site.
[b] Managed land was clearcut forest (logged <30 years ago) in the Staney and Steelhead study sites.

Table 2. Model selection results from mark–recapture analysis of Sitka black-tailed deer populations on Prince of Wales, Alaska, in 2006–2008, sampled using DNA extracted from fecal pellets.

Model no.	Model[a]	AIC_c[b]	ΔAIC_c	w_i[c]	K[d]	Deviance
1	*p*(*time* + *clearcuts*)	3950.6	0.00	0.36	9	3933
2	*p*(*time* + *clearcuts* + *stem-exclusion*)	3951.5	0.87	0.23	10	3931
3	*p*(*time*)	3952.2	1.56	0.17	8	3936
4	*p*(*time* + *stem-exclusion*)	3952.3	1.66	0.16	9	3934
5	*p*(*time* + *unmanaged land*)	3953.6	3.00	0.08	9	3936
6	*p*(*time1* + *clearcuts* + *stem-exclusion*)	3974.7	24.05	0.00	4	3967
7	*p*(*time1*)	3981.3	30.70	0.00	2	3977
8	*p*(*Time linear* + *clearcuts* + *stem-exclusion*)	4016.8	66.19	0.00	4	4009
9	*p*(*Time linear*)	4018.0	67.32	0.00	2	4014
10	*p*(*clearcuts* + *stem-exclusion*)	4023.1	72.51	0.00	3	4017
11	*p*(.)	4029.2	78.56	0.00	1	4027

[a] Model parameter definitions: *p* = capture probability, (.) = constant capture probability. Capture probability allowed to vary with *time* (each sampling occasion), *time1* (only first sampling occasion), *Time linear* (a linear trend during sampling occasions), and for deer marked in *unmanaged land* (unlogged forest), and both types of managed land, *clearcuts* (forest logged <30 years ago), and *stem-exclusion* (forest logged >30 years ago).
[b] Akaike's Information Criterion adjusted for sample size.
[c] AIC_c model wt.
[d] No. of parameters.

SE = 12.2%), and Steelhead (clearcut forest, $\Delta = -5\%$, SE = 20.9%) did not change from 2006 to 2008 (Table 1). Within sites and independent of habitat type, abundance estimates declined in Maybeso by 48% (SE = 8.5%) and in Staney by 24% (SE = 7.9%) but did not change in Steelhead ($\Delta = -11\%$, SE = 10.9%) from 2006 to 2008. Combining all sites and habitat types, deer abundance declined 30% (SE = 5.1%) from 421 (SE = 16.8) in 2006 to 295 (SE = 13.6) in 2008 (Table 1).

Combining all study sites across years, MMRDs ($\bar{x}$ = 443 m, SE = 61.0) were similar among individual deer ($\chi^2 = 5.186$, $P = 0.746$). Also, when we compared year and study site separately, estimates of MMRD were similar among study sites ($\chi^2 = 1.644$, $P = 0.440$) and among years ($\chi^2 = 1.959$, $P = 0.388$). Therefore, we assigned a 443 m strip boundary around all transects and calculated an effective sampling area of 8.8 km^2 (SE = 0.60), 16.8 km^2 (SE = 1.15), and 9.7 km^2 (SE = 0.67) in Maybeso, Staney, and Steelhead, respectively. Combining all sites and habitat types, our mean estimate of deer density declined 32% over the 3-year study, declining from 13.1 deer/km^2 (SE = 1.6) in 2006 to 8.9 deer/km^2 (SE = 1.2) in 2008 (Fig. 3).

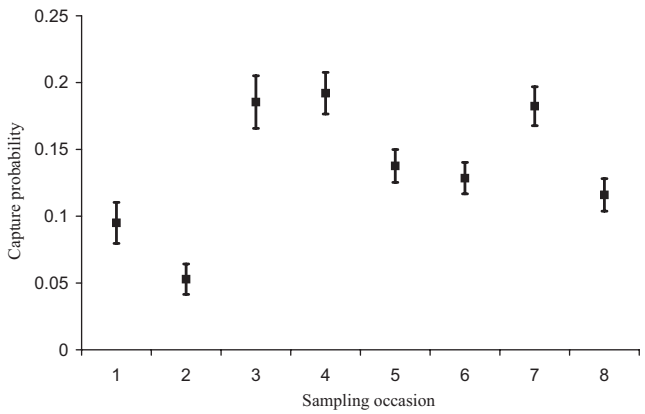

Figure 2. Estimates (error bars = SE) of capture probabilities using DNA from fecal pellets of Sitka black-tailed deer on Prince of Wales Island, Alaska, during consecutive sampling occasions. We combined data from study sites (Maybeso, Staney, Steelhead), years (2006–2008), and habitat (managed and unmanaged land).

Our effective sampling area for deer in managed land in Maybeso, Staney, and Steelhead was 4.7 km^2 (SE = 0.32), 5.9 km^2 (SE = 0.41), and 1.6 km^2 (SE = 0.11), respectively. Corresponding estimates of effective sampling area in unmanaged land in Maybeso, Staney, and Steelhead were 4.1 km^2 (SE = 0.28), 10.9 km^2 (SE = 0.75), and 8.1 km^2 (SE = 0.55). Combining sites and years (but analyzing habitat type separately) our mean estimates of deer density were 9.4 deer/km^2 (SE = 1.46) in managed land and 12.2 deer/km^2 (SE = 1.37) in unmanaged land (Fig. 3). Combining all sites, our estimates of deer densities declined by approximately 7.5 deer/km^2 (45%) from 2006 to 2008 in unmanaged land but did not change in managed land ($\Delta = -1$ deer/km^2, 10%). Within Maybeso during 2006, our estimates of deer densities in unmanaged land were more than double estimates of deer densities in unmanaged land in Staney and Steelhead (Fig. 3). In contrast, our estimates of deer densities during 2006 in managed land in Staney and Steelhead were double that in managed land in Maybeso (Fig. 3).

Across years, mean estimates of deer density were lower in stem-exclusion forest (Maybeso, 7.4 deer/km^2, SE = 1.32) than in clearcut forest (Staney and Steelhead, 10.4 deer/km^2, SE = 1.5). In contrast, our mean estimate of deer density in unmanaged land (20.5 deer/km^2, SE = 2.26) in our study site with stem-exclusion forest (Maybeso) was more than double the deer density in unmanaged land (8.2 deer/km^2, SE = 0.92) in watersheds with clearcut forest (Fig. 3).

DISCUSSION

Our findings suggest that non-invasive sampling is an effective method for monitoring deer in environments where direct observation is impractical. Our deer trail sampling protocol enabled us to encounter many pellet groups, and our genotyping success improved each year of our study. By the final year of our study, genotyping success (87%) became

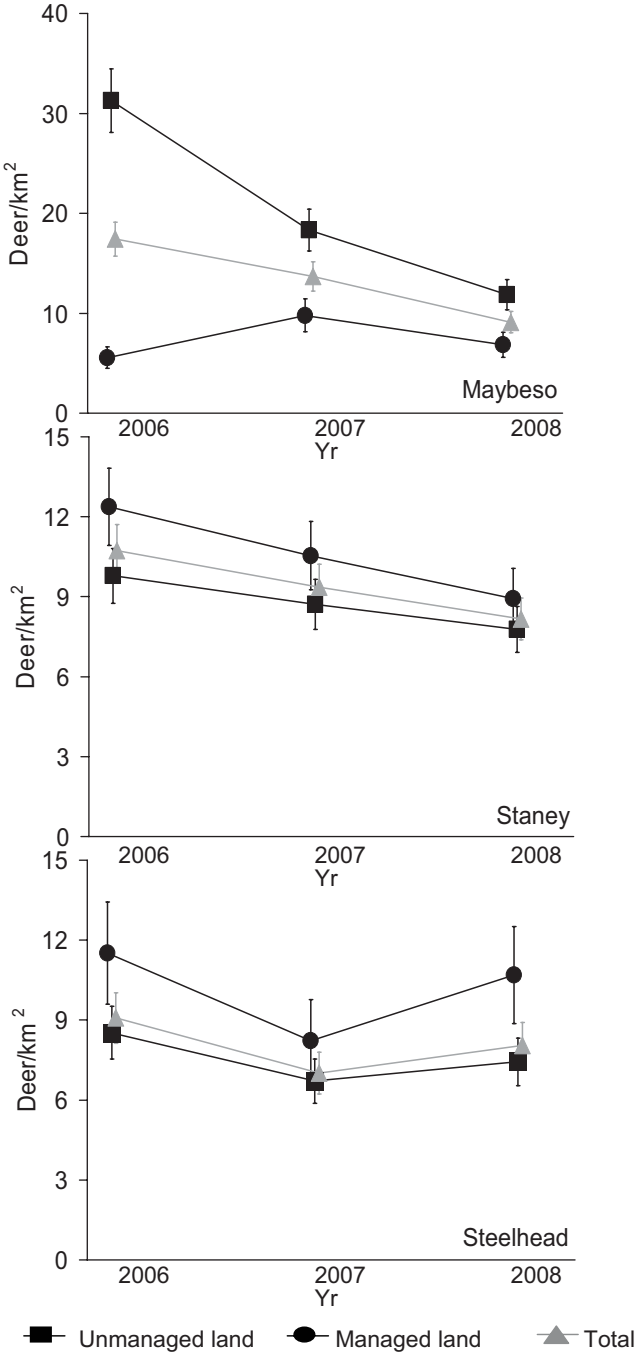

Figure 3. Density estimates (deer/km^2 ± SE) of Sitka black-tailed deer during 2006, 2007, and 2008 in 3 study sites (Maybeso, Staney, Steelhead) on Prince of Wales Island, Alaska. Managed land in Maybeso was stem-exclusion forest (logged >30 years ago). Managed land in Staney and Steelhead was clearcut forest (logged <30 years ago).

comparable to other non-invasive wildlife investigations (Hedmark et al. 2004 [65%], Belant et al. 2007 [75%], Kendall et al. 2008 [74%]). Increase in performance was likely influenced by optimization of extraction protocol, sampling fewer fecal pellets that appeared degraded during the first sampling occasion, and strictly adhering to 10-day intervals between sampling occasions (Brinkman et al. 2010). With the combination of high-encounter rates with pellets and high-genotyping success, mark–recapture estimates of deer abundance were feasible and efficient, even in the dense rainforest of Southeast Alaska.

We conservatively applied a simple closed model to our data. We chose this constrained approach to keep focus on our technique, to reduce confusion and data requirements associated with large numbers of parameters, and to take advantage of Program MARK's ability to draw off of multiple data sets to jointly estimate detection probability. Our erratic capture probabilities among sampling occasions (Fig. 2) help explain why the best models all incorporated parameters for time variation. The area of forest floor encompassed by one transect represents a small proportion of the total habitat used by deer while on winter range; thus, it is reasonable to expect that deer activity on our sampling area varied considerably during subsequent sampling occasions. Habitat covariates such as stem-exclusion forest and clearcut forest were included in the best-fit models, but the level of influence was minor relative to the differences in capture probabilities over time (i.e., sampling occasions). Models allowing capture probabilities to vary during the first sampling occasion received AIC_c weights $<1.0 \times 10^{-5}$, which suggests the persistence of pellets deposited over winter prior to sampling likely did not result in differences in capture probabilities between the first sampling occasion and subsequent capture occasions (Fig. 2). Rather, we speculate that pellets persisting through much of the winter that we collected during the first sampling occasion failed to yield sufficient DNA to be included in our analyses. The lack of support for our data with models that incorporated a linear-trend in time indicated that capture probability did not increase with each subsequent sampling occasion. Therefore, either pellet deposition rates by deer did not increase sufficiently with greening and growth of vegetation during our sampling period or the effects of an increase in deposition rates were minor relative to variation in capture probabilities over time because of other aspects of deer activity during our sampling period. Also, the lack of evidence of declining trends in capture probability over time supports our assumption that observer presence on transects every 10 days did not result in behavior differences in deer such as avoidance.

With our approach, we provide the first rigorous estimates of abundance and density with moderate precision (±20%) for Sitka black-tailed deer. It is difficult to compare our estimates of population density with other studies conducted in Southeast Alaska because most previous estimates were crude and often ad hoc extrapolations from pellet-count surveys that only focused on one habitat type or were limited data from spot-lighting surveys. Nonetheless, Sitka black-tailed deer densities have been estimated for deer on winter range in unmanaged land (29–57 deer/km^2, Smith and Davies 1975 *in* Herbert 1979; 10–23 deer/km^2, Herbert 1979; 12 deer/km^2, Wallmo and Schoen 1980; 19 deer/km^2, McNay and Doyle 1987; 34 deer/km^2, Kirchhoff 1994) and mixed unmanaged and clearcut forest (7–8 deer/km^2, USDA 1997) in various locations within the coastal forests of British Columbia and Alaska. Our estimates of deer densities (6–31 deer/km^2) using DNA-based

mark–recapture techniques fall within the range of previous estimates. However, our density estimates represent deer confined to winter ranges during late winter and early spring, which typically comprised about 83% of the total habitat available to deer during snow-free months. Consequently, our density estimates might be reduced by 15–20% if computed for all deer habitat available during summer within our study areas.

We compared estimates in managed and unmanaged land and determined that age of managed land influenced deer abundance and density. Whereas our estimates of deer density in clearcut forest was equal to or exceeded estimates in unmanaged land when compared within the same watershed within the same year, stem-exclusion forest (Maybeso) consistently supported the lowest densities of deer. High densities in clearcut forest and low densities on stem-exclusion forest likely reflect the steep decline in forage biomass as a young clearcut transitions into second-growth forest, whereas stem-exclusion forest often contains sparse understory forage important to deer (Alaback 1982, Hanley 1993).

Sitka black-tailed deer are at the northern extent of the range of the genus *Odocoileus*, populations of which are strongly influenced by snow depth and persistence (Klein 1965, Wallmo 1981, Parker et al. 1999, White et al. 2009). Mean estimates of deer density declined by approximately 30% over the 3-year study, and we speculate that this was caused by consecutive mild winters followed by consecutive harsh winters during our study period. During 2006–2008, winter snowfall in the region was 37% greater than the average for the previous 6 decades; furthermore, 3 consecutive harsh winters have not occurred consecutively since the 1970s (Alaska Climate Research Center 2009). Moreover, before 2006, winter snow depths were below average for several years.

Without reliable methods for estimating ungulate abundance in densely vegetated environments, we developed and evaluated field and laboratory sampling procedures that potentially can yield dependable and precise estimates for monitoring populations across a wide range of spatial and temporal scales. Because our study was the first broad-scale application of several new field and laboratory procedures, through trial and error, we identified several ways to improve the design of future studies. We suggest more experimentation and tests of assumptions within sampling design, genetic analysis, and modeling components of our study design.

Although a well-defined deer trail network was present in all habitat types, we quantified density of the trail system only in unmanaged land. We suggest that future studies evaluate trail density along with use or avoidance of trail systems at finer spatial scales and across all habitat types. If differences are evident, we suggest development of a correction factor or comparisons of relative rather than absolute ungulate densities. Additional evaluation of ways to increase encounter rates with fecal pellets without compromising statistical randomness and repeatability will reduce bias and assumptions. Specifically, we encourage exploration of the application of animal trail transects. The lack of thick vegetation on deer trail transects had several advantages over traditional straight-line transects including: applicability in all habitat types, better pellet-detection rates, easier travel through thickly vegetated habitats, and greater repeatability. For example, we would not have been able to survey young clearcut habitat or precommercially thinned young growth stands without this technique because dense regeneration and slash piles prevented us from following straight-line transects.

Careful attention should be given to the layout of sampling transects to reduce assumptions associated with density estimates. Varying distances among our transects did not create opportunities for recaptures along a continuum of distances in all directions, which precluded use of maximum likelihood methods to establish effective sampling area ($\hat{A}$, Otis et al. 1978). We suggest experimenting with a grid-like array of transects to better-fit likelihood-based estimators of density (Program DENSITY, Efford et al. 2004) calculated using spatially explicit capture and recapture data. Also, new approaches have been developed to incorporate adaptive sampling into modeling frameworks. Conroy et al. (2008) proposed a Bayesian 2-phase sampling approach to estimate abundance in patchily distributed animal populations. The approach of Conroy et al. (2008) would be particularly useful when the sampling of all habitat types is not possible, yet extrapolation to larger scales is necessary.

Rather than incorporating genotyping error into our statistical models, we excluded samples and genetic loci that showed signs of error. The cost of this approach was that we lost information when we discarded samples with some degree of error in their genotype. It may be beneficial to test the performance of misidentification models (Lukacs and Burnham 2005). Misidentification models address uncertainty associated with including samples and genetic markers with some degree of genotyping error. That approach may increase sample size and reduce costs associated with re-analyzing the same sample several times to reach a consensus genotype. Other viable approaches for accounting for genotype uncertainty also exist (e.g., Miller et al. 2002, Wright et al. 2009).

Lastly, our DNA-based estimates of abundance and density have not been tested against true densities and genotypes of deer. Forsyth et al. (2007) compared relationships between fecal pellet indices and true deer density. Creel et al. (2003) compared a census of fecal genotypes with blood genotypes and known numbers of wolves. We suggest further investigations of DNA-based estimates using similar approaches. Although nearly impossible in some environments for some taxa, testing against known numbers may be the only way to fully validate our technique.

MANAGEMENT IMPLICATIONS

Our DNA-based technique should be useful to wildlife biologists seeking to monitor ungulates in densely vegetated environments where direct observation is difficult or in areas where invasive approaches are less acceptable. Further, our sampling design provides wildlife biologists with an approach that should increase encounter rates with pellet

groups and foster the use of mark–recapture methods to estimate population parameters. The precision of our estimates of abundance (±20%) may be particularly appealing to wildlife managers mainly relying on pellet-count surveys to monitor ungulate populations. We encourage future experimentation with trail transects to improve density calculations and to test statistical inference.

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