



Original Article

Estimating Abundance of a Cryptic Social Carnivore Using Spatially Explicit Capture–Recapture

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ABSTRACT Estimating population abundance of wolves (*Canis lupus*) in densely forested landscapes is challenging because reduced visibility lowers the success of methods such as aerial surveys and enumeration of group size using radiotelemetry. However, regular population estimates of wolves are necessary for population monitoring and sustainable management. We used noninvasive hair snaring and spatially explicit capture–recapture (SECR) to estimate wolf abundance on Prince of Wales Island (POW), Alaska, USA, during 2012–2015. We monitored 36–82 hair-snare stations weekly for 9–11 weeks during autumn. The noninvasive study area covered 1,683 km² during 2012–2013 and was expanded to 3,281 km² during 2014–2015. We identified 57 individual wolves during the study period using DNA from hair follicles genotyped at 10 microsatellite loci. We used population density estimates using SECR (2013: 24.5 wolves/1,000 km² [95% CI = 14.4–41.9 wolves/1,000 km²], 2014: 9.9 wolves/1,000 km² [95% CI = 5.5–17.7/1,000 km²], 2015: 11.9 wolves/1,000 km² [95% CI = 7.7–18.5 wolves/1,000 km²]) to predict the autumn population for the POW management unit (2013: 221.1 wolves [95% CI = 130–378]; 2014: 89.1 wolves [95% CI = 49.8–159.4]; 2015: 107.5 wolves [95% CI = 69–167]). We detected and redetected more wolves and increased the precision of the density estimate after increasing the hair sampling intensity and sampling area in 2014–2015. Our results demonstrate that estimating wolf abundance using noninvasive sampling and SECR was feasible and reliably applied producing a statistically robust population estimate for monitoring wolf populations in densely forested areas. These methods have promise for application to widely ranging carnivores at population-level scales and may be especially useful when regular density estimates are necessary for management and conservation. © 2019 The Wildlife Society.

KEY WORDS *Canis lupus*, monitoring, noninvasive genetic sampling, population estimation, spatially explicit capture–recapture, wolf.

Estimating population abundance of carnivores in densely forested landscapes is challenging because of their cryptic nature, including nocturnal behavior, avoidance of humans, large home-range areas, and low densities. Wolves (*Canis lupus*) are renowned as one of the most difficult species to survey, particularly in areas with dense forest cover and lack of snow (Boitani 2003). One of the most common means to estimate wolf density is aerial telemetry of marked individuals, wherein wolves are radiocollared from every

pack in the survey area, minimum counts of pack sizes are obtained visually through aerial observations, and the total number of wolves is divided by the sum of the pack territory areas (i.e., territory mapping; Peterson et al. 1984, Fuller 1989, Hayes 1995). The aerial radiotelemetry approach has been widely used since the 1970s and remains commonly applied in areas with open terrain (Ballard et al. 1997, Hayes et al. 2003, Adams et al. 2008, Lake et al. 2015, Boertje et al. 2017). This method is effective if a sufficient number of wolves are radiocollared and monitored in all adjacent packs in a region (Burch et al. 2005); yet, meeting these requirements is generally expensive, time-consuming, and difficult to apply over a large area (Boitani 2003, Schmidt et al. 2017). This method is also less successful in areas with

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thick forest canopies that hinder visibility, when wolf populations are large, or when pack turnover is high due to mortality. Aerial snow-tracking is another widely used method to survey wolves (Gasaway et al. 1983, 1992; Hayes et al. 2003; Gardner and Pamperin 2014; Kojola et al. 2014). Snow-tracking is most effective in open or semiforested terrain, although this method has been used in forested landscapes at high expense (Patterson et al. 2004). Snow-tracking also requires consistent snow cover during the survey period. In many regions occupied by wolves, snow cover is variable or absent, particularly in temperate areas (Blanco and Cortés 2012, Liberg et al. 2012). However, regular population estimates of wolves are necessary, even more so in areas where there is elevated concern for population management or conservation.

In southeastern Alaska, USA, wolves inhabit temperate rainforests distributed across the mainland coast and most large islands south of Frederick Sound (Fig. 1). Concerns about the conservation status of wolves in southeastern Alaska have intensified the relevance of obtaining current population estimates. Attention has largely focused on Prince of Wales Island (POW; Fig. 1), containing

approximately one-third of the southeastern Alaskan wolf population (Person et al. 1996). The U.S. Fish and Wildlife Service (USFWS) conducted 12-month Endangered Species Act reviews of the Alexander Archipelago wolf (*C. l. ligoni*) on 3 occasions in the past 2 decades (USFWS 1995, 1997, 2016). Although listing was determined not warranted at the time of the decisions, these reviews raised questions about the long-term viability of POW wolves because of declining habitat quality and human harvest.

The U.S. Forest Service (USFS) manages the Tongass National Forest, which encompasses the majority of the land in southeastern Alaska. The wolf is a management indicator species in the Tongass National Forest Land and Resource Management Plan (USFS 1997, 2008). Recently, the USFS developed forest-management recommendations for maintenance of sustainable wolf populations (Wolf Technical Committee 2017). In 2014, the Alaska Department of Fish and Game (ADF&G) responded to concerns over the POW wolf population by reducing wolf harvest in Game Management Unit 2 (GMU 2; encompassing the POW Island complex; Fig. 1) to 20% of the autumn population estimate from the previous 30% limit.

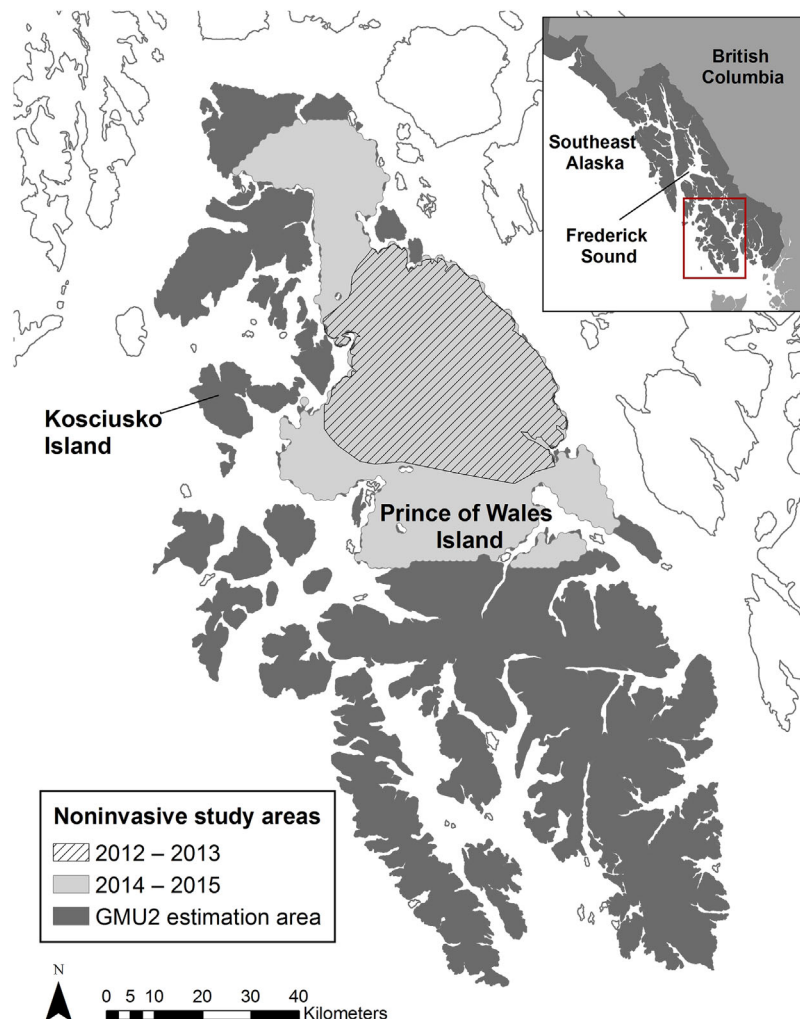


Figure 1. Study area for wolf population estimates using noninvasive hair snaring to collect DNA for spatially explicit capture–recapture, Prince of Wales Island, Alaska, USA, 2012–2015. GMU2 is Game Management Unit 2.

Until this study, the most recent autumn wolf-population estimate was $\hat{N} = 269$ (SE = 80) for a portion of GMU 2 (POW and Kosciusko Islands = 6,808 km²; Person et al. 1996). The estimate was produced using radiocollared wolves to locate packs and aerially count the pack members (Person et al. 1996). Population estimation was not repeated in following years because of the expense and high intensity of effort required to maintain and monitor a sample of radiocollared wolves on POW. However, regular population estimates at shorter intervals are desirable for monitoring populations and evaluating management strategies to ensure they are sustainable. To address this information gap, we sought to rigorously test an alternate population estimation technique that could be applied in this environment. Genetic capture–recapture using DNA from hair has been used to estimate population abundance of cryptic species living in dense forests (Kendall et al. 2008, Russell et al. 2012, Morton et al. 2016), including wolves (Stenglein et al. 2010; Ausband et al. 2011, 2014; Stansbury et al. 2014). The development of spatially explicit capture–recapture techniques (SECR; Efford 2004) has provided a means to estimate animal density by incorporating spatial detection histories of individual animals from locations of animal captures and movements. The spatial detection histories are used to fit a spatial model representing the distribution of the animal home ranges (the state model), and a spatial model of the detection process (the observation model). The probability of detecting an animal is then related to the distance between its activity center and the detector. Successful application of SECR requires multiple recaptures of the same individuals in different locations; therefore, it was necessary to assess our ability to detect and redetect individual wolves from noninvasive samples. Wolves, like many large carnivores can exist at relatively low densities, and their cryptic nature can contribute to sparse data sets (Russell et al. 2012). For robust parameter estimation (resistant to violations of model assumptions) using spatial-capture–recapture a sample size of ≥ 20 recaptures is recommended (Efford 2004, Efford et al. 2009). Even at these low captures rates, estimates of the range parameter σ have negligible bias (0.75%), though precision is substantially greater as capture rate increases (Borchers and Efford 2008).

Wolves are social carnivores and their behavior patterns may contribute to several unique situations that are necessary to consider in a study design. Wolves function as a pack and share the same home range, so their individual movements may not be independent. The SECR method assumes that the distributions of animal activity centers and animal movement are independent; therefore, social carnivore behavior such as group aggregation and territoriality violate this assumption. Although mean parameter estimates are not likely to be affected, violating this assumption results in overdispersion; thus, variance estimates would be biased low with 95% confidence intervals that are narrower than they would be otherwise (Efford 2004). Scenarios of nonindependence and spatial aggregation of individual wolves were assessed in simulation analyses by López-Bao et al. (2018) and results indicated only a slight underestimation in

population abundance of spatially aggregated individuals in comparison to independently distributed individuals. Therefore, aggregation of social carnivores in packs and movement patterns centered on pack territories should have only a minor effect on density estimates. However, further research on this topic would be beneficial for informing approaches to estimating density of group-living animals. Beginning in 2012, we initiated a project to address the need for timely and accurate wolf population information. We also conducted an evaluation of the extent of sampling area, sampling frequency, and density of sampling stations required to obtain robust population estimates along with the corresponding effort. We used DNA samples collected from hair to estimate autumn density using a SECR approach (Efford 2004, Borchers and Efford 2008, Kery et al. 2011, Royle et al. 2011). Additionally, we explored effects of increasing the extent and intensity of sampling on density estimates.

STUDY AREA

Prince of Wales was the largest island (6,670 km²) in the southern portion of the southeastern Alaska Archipelago (Fig. 1). This land mass contained rugged mountains $\leq 1,160$ m, multiple watersheds, and large tracts of temperate rain forests dominated by Sitka spruce (*Picea sitchensis*) and western hemlock (*Tsuga heterophylla*) at elevations below 600 m (Alaback 1982). Old-growth forest was distributed in a matrix interspersed with even-aged forest stands at different successional stages resulting from clearcut logging. Annual precipitation, mostly as rain, ranged from 130 to 400 cm, with intermittent snow during the winter months. Northern POW has the greatest rates of logging in southeastern Alaska (Albert and Schoen 2013). Approximately 4,800 km of roads were built throughout POW to facilitate logging, with the greatest road densities in northern POW (0.49–1.04 km/km²; Person and Russell 2008, Person and Logan 2012). Prior to this study, high levels of wolf harvest (1.7–14.3 wolves/1,000 km², 2000–2009; Person and Logan 2012) occurred on northern POW. During 2012–2013, the wolf-capture and hair-collection study area covered 1,683 km² in the north-central portion of POW, representing approximately 20% of Game Management Unit 2 (GMU 2; Fig. 1). During 2014–2015, we increased the extent of our noninvasive DNA sampling area to 3,281 km², representing approximately 36% of GMU 2 (Fig. 1).

METHODS

Sample Collection

During autumn 2012–2015, we established an array of sampling nodes consisting of 5 hair boards (i.e., hair-snaring devices) set at 50-m spacing intervals across the study area (Fig. 1). Node spacing was roughly 3.9 ± 1.1 km during 2012–2013, and 3.5 ± 1.0 km during 2014–2015. Hair board nodes were deployed mid-October–late-December (2012, $n = 37$; 2013, $n = 36$; 2014, $n = 72$; 2015, $n = 82$). In a design modified from Ausband et al. (2011), we constructed hair boards from plywood and affixed barbed-wire and tie-wire to create snagging surfaces (Roffler et al. 2016). We

applied approximately 5 mL of commercially produced lure to the hair boards on every sampling occasion to evoke a scratch-and-rub response (Fig. 2). We stabilized boards with 16 penny nails driven through the corners of the board and into the ground and attached the boards to a flagged tree or branch with wire. Sampling intervals were 10 days in 2012 and 7 days in 2013–2015. We reduced the length of time between node checks beginning in 2013 to minimize potential genotyping error from DNA degradation (e.g., from moisture), and increase our chances of redetecting individual wolves. Hair was collected using sterilized tweezers, stored in labeled coin envelopes, and dried at room temperature. To prevent cross-contamination we used a soldering torch to sterilize hair board barbs after collecting hair samples.

Genotyping

We conducted DNA extractions, genetic identification of species, wolf genotyping, and sex identification at the National Genomics Center for Wildlife and Fish Conservation, Missoula, Montana, USA. For DNA extractions, we used 10–20 hairs, except in situations when we had evidence of >1 wolf depositing hair on the same board (multiple wolves detected in photos, multiple sets of tracks, or from very large clumps of hair collected on a board). In these cases, we implemented a single-hair DNA extraction protocol to detect multiple individuals from these samples and eliminate the chance for mixed-DNA samples, which would increase genotyping error. This protocol consisted of selecting 4 hairs with follicles from different locations in the hair clump and performing a separate DNA extraction on each hair. We extracted DNA from samples using standard protocols for tissues (DNeasy Blood & Tissue kit; Qiagen, Valencia, CA, USA) with the following modifications: overnight incubation in buffer ATL and Proteinase K on a rocker or in a rotating oven at 56°C, a 70°C incubation for 10 min after adding buffer AL, and a final elution using 100 µL buffer AE warmed to 70°C.

We first identified samples to the genus level by Sanger sequencing a portion of the 16S rRNA gene from the mitochondrial genome (mtDNA) to screen nontarget species. We amplified the 16S rDNA using conserved, universal primers 16sL 5'-TTAAACGGCCGCGGTATCC-3' and 16sR 5'-GAATTACGCTGTTATCCCT-3' modified from Hoelzel and Green (1992). The mtDNA analysis does not distinguish between wolves and dogs (*C. l. familiaris*), but we were able to screen dogs from the final data set after microsatellite genotyping as described in the following 3 paragraphs.

We used muscle tissue samples from wolves taken during annual hunting and trapping seasons and blood samples from 10 wolves captured during radiocollaring to design the microsatellite panel and distinguish wolves and dogs in the noninvasive sampling. These samples were not used in any of the population estimates. Ten loci were variable in our wolf population and amplified consistently in noninvasively collected DNA samples: cph5 (Fredholm and Wintoro 1995); fh2096, fh2137, fh2054, fh2140, fh2161, Pez17, fh2001 (Duchamp et al. 2012); fh2079 (Francisco et al. 1996); c20.253 (Ostrander et al. 1993). We calculated the probability of identity ($P_{(ID)}$) and probability of identity for siblings ($P_{(ID)sibs}$) using GenAlEx 6.5 (Peakall and Smouse 2006).

We first amplified all canid hair DNA samples at 2 loci that amplify most consistently in noninvasive samples (cph5 and fh2096) and included 2 positive controls in each PCR. Samples that amplified consistently at one or both loci were then amplified at the remaining 8 loci (the others were discarded from further analysis). We accepted data for each sample at each locus only if the sample amplified consistently between duplicates. If amplification was inconsistent between duplicates (e.g., 3 alleles detected in one or both duplicates, allelic drop out, or false alleles), no genotype was called for that locus. We amplified samples with missing genotypes at <4 loci in duplicate at those loci. Consistent amplification was required in ≥ 2 amplifications before a



Figure 2. Wolf rubbing on hair-snare board, Prince of Wales Island, Alaska, USA, 2012–2015.

consensus genotype was called. We added negative controls to all steps in 2015, and contamination was not detected. We quantified genotyping error as the proportion of PCR reactions at all loci with allelic dropout or the amplification of false alleles. We quantified genotyping success rate as the percentage of samples that successfully amplified and passed quality control steps for 1) identifying individual wolves out of all the hair samples; and 2) identifying individual wolves from all the hair samples identified as canids. We used MicroChecker 2.2.3 with 1,000 randomizations to identify genotyping errors including null alleles, stutter, and allelic dropout (Van Oosterhout et al. 2004). We used DROPOUT 2.3 to identify matches of unique genotypes within and among sampling seasons (McKelvey and Schwartz 2005). We identified sex of individual wolves using the canid SRY marker (Wictum et al. 2013).

We used 2 methods using reference data from local wolves and dogs to differentiate wolves from dogs with microsatellite data. First, we conducted a principal coordinate analysis (PCoA) to visualize clustering (GenAlEx 6.5). Second, we used a Bayesian clustering procedure implemented in STRUCTURE v2.3.3 to assess the average proportion of membership of the sampled canids to either the wolf or dog clusters (Pritchard et al. 2000). We assumed 2 populations ($K=2$) with a general admixture model and correlated allele frequencies and performed the analysis 10 times independently after a burn-in of 100,000 and 1,000,000 Markov Chain Monte Carlo repetitions.

Population Density Estimates

We used SECR models in the Program R software package SECR (v 2.9.4; Efford 2015) to estimate the density and population size of wolves in our study area (Efford 2004, Borchers and Efford 2008). We compiled spatial detection histories for wolves genetically identified from hair deposited on hair boards on multiple sampling occasions. We defined sampling occasions as the period between node checks and allowed the length to vary for each node individually based on actual node exposure time. A few nodes could not be checked during a sampling occasion because of severe snow conditions; thus, we considered the node inactive during that occasion, but we then increased the length of the subsequent occasion to account for the actual exposure time. We specified a clustered trap design, so unique detections at all 5

hair boards within a node could be used individually for parameter estimation. We fit models specifying count type detectors because multiple wolves could be detected at the same hair board during the same occasion, and the same wolf could be detected at multiple locations during the same occasion. We fit hybrid mixture models with a Gaussian detection probability function and incorporated covariates including sex and a variety of coefficients representing the effects of various behavioral responses and site-specific changes in effectiveness on detection probability and movement parameters (Pledger 2000; Table S1, available online in Supporting Information). We evaluated a suite of competing models based on information theoretic methods (Akaike's Information Criterion corrected for small sample size [AIC_c]; Burnham and Anderson 1998).

We defined a discrete habitat mask based on a 500-m grid for the study area by delineating a buffer around the trap array (based on the maximum extent of animal movement during the study period) and then clipped it to the POW shoreline (Fig. 1). The buffer was 10 km in 2012 and 2013, and 20 km in 2014 and 2015, resulting in 1,683 km² and 3,281 km² study areas, respectively. We used wolf density estimates from the study area to predict the GMU 2 (9,025 km²) wolf abundance. We assessed significant differences ($\alpha=0.05$) in SECR model parameter estimates between years by generating bootstrapped 95% confidence intervals of the difference between estimates on the original log scale using 5,000 replications.

RESULTS

Sample Collection

We collected 64 hair samples from hair boards in 2012, 93 in 2013, 147 in 2014, and 232 in 2015 (Table 1). The number of wolves redetected increased throughout the study period (2012: $n=6$, 2013: $n=8$, 2014: $n=10$, 2015: $n=15$). To assess the contribution of increased sampling area and intensity on success of detecting individual wolves, we compared 2014 and 2015 sampling results using all the nodes (2014: $n=72$, 2015: $n=82$) to results using data from only the nodes previously used in 2013 ($n=34$; 3 nodes could not be reestablished during 2014–2015 due to road closures or construction). Trapping success (no. of wolf detections via DNA/100 trap-nights) was not greater with increased

Table 1. Number of hair samples collected, the percentage of samples successfully identified to the genus level using mtDNA, the percentage of 1) all the hair samples; and 2) the *Canis* spp. hair samples successfully identified to the individual level using 10 microsatellite loci, the number of hair samples that successfully identified individuals, the number of individual wolves identified from hair samples, and the male (M) and female (F) wolves sampled by year on Prince of Wales Island, Alaska, USA, 2012–2015. “NA” is not applicable.

Year	No. of hair samples	Genus ID success	Individual ID success	Individual ID success (canids only)	No. of hair samples ID success	No. of wolves detected	M	F
2012	64	81%	39%	67%	30	11	9	2
2013 ^a	80	91%	56%	83%	45	18	8	10
2013 ^b	52	NA	23%	NA ^c	12	7 ^d	4	3
2014	147	71%	45%	65%	65	21	14	7
2015	232	79%	46%	78%	106	24	12	12

^a Regular hair DNA extractions.

^b Single-hair DNA extractions.

^c No genus ID.

^d Four individuals also represented in regular extractions.

Table 2. Sampling effort for spatially explicit capture–recapture estimates of wolf density using noninvasively collected wolf hair, Prince of Wales Island, Alaska, USA, 2012–2015.

Year	Total days	No. of hair-snare nodes	Wolves detected ^a	Wolves/100 trap-nights
2012	69	38	16	1.32
2013	68	37	33	1.88
2014	66	72	37	0.84
2014 ^b (2013 nodes)	66	34	21	1.00
2015	76	82	56	1.09
2015 ^b (2013 nodes)	76	34	23	0.86

^a The total number of wolf detections (includes redetections).

^b These nodes were a subset sample for comparison with the same nodes sampled in 2013.

sampling effort, but we did detect more wolves in the expanded study area in comparison to the reduced study area (Table 2).

Genotyping

Genus identification was performed on mtDNA sequences from all collected hair samples, with the exception of the 13 hair samples collected in 2013 on which we performed the single-hair extraction protocol (see third paragraph in this section). Genus identification success ranged from 71 to 91% (Table 1; Table S2, available online in Supporting Information).

Using microsatellites from the harvested wolves, the putative wolves identified from hair samples, the 59 known dogs, and the 18 suspected dogs including 2 recaptures (5 in 2012, 6 in 2013, 4 in 2014, and 5 in 2015), we demonstrated that the dogs clustered together and apart from the known wolf samples, as well as apart from the wolves identified from hair samples (Fig. S3, available online in Supporting Information). Samples from the putative dogs contained alleles at 3–6 loci that were consistent with known dogs and that we did not observe in our known wolf samples. The STRUCTURE clustering was consistent with PCoA results with dogs and wolves clearly separated (data not shown). Average population assignments were large for each group ($q = 0.99$ for both dogs and wolves). These analyses suggest the 18 individuals were dogs and not wolves; thus, they were excluded from subsequent analyses.

The 10 variable microsatellite loci produced a cumulative $P_{(ID)} = 5.35 \times 10^{-7}$, and $(P_{(ID)sibs}) = 1.9 \times 10^{-3}$, providing acceptable power to identify individuals and siblings from the noninvasive samples. We used the microsatellite panel to genotype hair samples identified as canids. Genotyping error occurred in 3.3% of the first duplicate reactions at all loci, and 2.9% in a rerun of a second duplicate. The genotyping success rate (the percentage of samples that successfully amplified and passed quality control steps) of identifying individual wolves out of the regular extractions for all hair samples ranged from 39 to 56%. The genotyping success rate of identifying individual wolves from only the canid hair samples ranged from 65 to 83% (Table 1). The single-hair extraction samples had a considerably lower genotyping success rate for identifying individuals at 23%, although 7

individuals were identified (4 were represented in the standard hair extraction samples, and 3 were previously undetected wolves; Table 1).

During the time period of the hair board sampling, 57 wolves were identified from noninvasively collected hair samples. Nine wolves were detected across sampling years from hair samples; 4 of 24 wolves detected in 2015 had been previously detected in 2013 and 2014. The 8 redetected wolves in 2013 consisted of 4 individuals detected twice, and 4 individuals detected 3 times. The 10 redetected wolves in 2014 included 5 individuals detected twice, 3 individuals detected 3 times, and 2 individuals detected 6 times. Of the 13 redetected wolves in 2015, 6 individuals were detected twice, 4 individuals were detected 3 times, and 2 individuals were detected 4 times, and 1 individual 6 times. The distance between sequential redetections at hair board nodes in 2013 ranged from 0 (recaptured at same node where originally detected) to 27.7 km (mean distance = 2.9 ± 5.9 km); whereas, in 2014, distances moved were larger (range = 0–29.6 km; mean distance = 17.9 ± 1.6 km). In 2015, the maximum distance moved between a consecutive redetection was large, though the average distance was smaller than in 2014 (range = 0–41.7 km, mean 8.4 ± 10.4 km).

We did not detect allelic dropout or stuttering in the microsatellite loci, but 2 of the 10 loci (fh2137 and fh2001) demonstrated a significant probability of homozygote excess (in one of 11 and one of 10 alleles, respectively) signifying the possibility of null alleles. Inbreeding can also contribute to development of homozygote excess; therefore, we used Null Allele Estimator 1.3 to account for the bias of inbreeding in null allele estimates (Van Oosterhout et al. 2006). Using estimates of inbreeding ($F_{IS} = 0.051$; described below), we determined the frequency of null alleles was 0.012 across all 10 loci and thus we retained them for further analyses.

Population Density Estimates

Sampling during 2012 resulted in an insufficient number of redetections of individual wolves from hair samples for a reliable population density estimate (only 5 wolves were redetected after initial detection). The density estimate from the autumn 2013 top-ranked SECR model was 24.5 ± 6.8 wolves/1,000 km² (95% CI = 14.4–41.9 wolves/1,000 km²; CV = 0.278; Table 3). This model included a sex-specific coefficient on both the baseline detection probability parameter (g_0) and the range parameter (σ), which is related to, and proportional to, the size of the home range. The top-ranked model for 2013 also incorporated a site-effectiveness coefficient (k) on g_0 . This term indicated that the probability of detecting an animal at a given location increased by 4.7 ± 1.5 times after the first detection (i.e., the site became more effective). Using the density estimate from the top-ranked model, the estimated autumn 2013 population size of the study area (1,683 km²) was 41.3 ± 11.7 wolves (95% CI = 24.0–71.2), and the predicted population size for GMU 2 was 221.1 ± 61.4 wolves (95% CI = 130.0–378.1).

The density estimate for autumn 2014, based on the top-ranked model, was 9.9 ± 3.0 wolves/1,000 km² (95% CI = 5.5–17.7 wolves/1,000 km²; CV = 0.304; Table 3). This

Table 3. Comparison of density estimates of autumn wolf population, based on the most parsimonious spatially explicit capture–recapture hybrid mixture model using data from the full sampling node array, and the truncated array (using sampling nodes established in 2013), 2013–2015, Prince of Wales Island, Alaska, USA. Predicted wolf population estimates for Game Management Unit (GMU) 2 (9,025 km²) are shown. SE, standard error; CI, confidence interval.

Year	No. of nodes	Area (km ²)	Density (per 1,000 km ²)		CV _D	GMU 2 expected $\hat{N}$
			Density $\pm$ SE	95% CI		$\hat{N} \pm$ SE
2013	37	1,683.8 km ²	24.5 $\pm$ 6.8	14.4–41.9	0.278	221.1 $\pm$ 61.4
2014 (all nodes)	72	3,280.9 km ²	9.9 $\pm$ 3.0	5.5–17.7	0.304	89.1 $\pm$ 27.1
2014 (2013 nodes)	34	1,689.4 km ²	10.7 $\pm$ 4.1	5.2–21.9	0.383	96.5 $\pm$ 35.2
2015 (all nodes)	82	3,281.1 km ²	11.9 $\pm$ 2.7	7.7–18.5	0.228	107.5 $\pm$ 24.4
2015 (2013 nodes)	34	2,463.6 km ²	17.0 $\pm$ 10.5	5.0–57.6	0.621	153.7 $\pm$ 95.6

estimate was significantly lower than the previous year. In contrast to 2013, where the top model accounted for 100% of the AIC_c weight, there were several competing models for 2014. The top-ranked model for 2014, which had an AIC_c weight of 0.378, also contained a site-effectiveness term on the baseline detection probability and indicated an increase in $\hat{g}_0$ of 4.9 ± 1.6 times after the first detection at a given location. Using the density estimate from only the top-ranked model, the predicted number of wolves in the 2014 extended study area (3,281 km²) was 32.4 ± 10.1 (95% CI = 17.9–58.7) and 89.1 ± 27.1 (95% CI = 49.8–159.4) for GMU 2.

The density estimate from the autumn 2015 top-ranked SECR model was 11.9 ± 2.7 wolves/1,000 km² (95% CI = 7.7–18.5 wolves/1,000 km²; CV = 0.228; Table 3). The top 5 population estimate models for 2015 wolf density in the study area resulted in similar estimates and all contained either a site-effectiveness (k) or site-specific behavioral change (bk) coefficient on g_0 . Using the density estimate from the top-ranked model to predict the number of wolves in the extended study area (3,281 km²) resulted in an estimate of 42.5 ± 6.3 wolves (95% CI = 33.7–59.6), and a population estimate in GMU 2 of 107.5 ± 24.5 wolves (95% CI = 69–167). This estimate is significantly greater than the autumn 2014 estimate.

To examine effects of expanding the study area and sampling intensity in 2014, we fit models with the same parameter specifications using a reduced data set containing information only from nodes that had also been deployed in 2013. Similar to 2013, a 10-km buffer was used based on an analysis of the animal movements among the reduced set of nodes. The top-ranked model using the reduced data set was similar to the top-ranked full-data model, except that the site-effectiveness term was a transient response (K) where the change in site effectiveness depends on the preceding occasion, rather than a change that persisted throughout the remainder of the study period. The density estimate using this model was greater (10.7 ± 4.1 wolves/1,000 km², 95% CI = 5.2–21.9 wolves/1,000 km²) than the top-ranked full-data model (9.9 ± 3.0 wolves/1,000 km²), but not significantly so (Table 3). The predicted population in the study area based on this density estimate was comparable to that defined in 2013 (i.e., with a 10-km buffer) of 18.1 ± 6.8 wolves (95% CI = 8.8–36.9). Using this density estimate to predict the 2014 population size for GMU 2 resulted in an estimate of 96.5 ± 35.2 wolves (95% CI = 48.3–193.0;

Table 3). Increasing the size of the study area and the density of nodes resulted in a density estimate with a substantially lower coefficient of variation for the estimated density parameter (0.304 vs. 0.383).

A similar analysis was performed for the 2015 data; however, a 20-km buffer was used because of some extremely large movements made by a small subset of animals. The formulation of the top-ranked model for the reduced data set (using information only from the nodes deployed in 2013) was the same as the top-ranked model using the full data set. The density estimate produced using this top-ranked model with the reduced data set was greater (17.0 ± 10.5 wolves/1,000 km², 95% CI = 5.0–57.6 wolves/1,000 km²) than the full-data model (11.7 ± 2.7 wolves/1,000 km²; Table 3). Using the reduced-data-set density estimate, the GMU 2 population size was predicted to be 153.7 ± 95.6 wolves (95% CI = 50.1–471.4); however, precision was low (CV = 0.621; Table 3). Therefore, expanding the study area and the density of nodes in 2015 (compared with 2013) resulted in a much more precise population estimate.

DISCUSSION

Our objective was to assess the use of a noninvasive sampling and SECR approach to estimate abundance of wolves over a multiyear period in a dense rainforest environment. We conducted this research to evaluate whether this method would be more reliable (produce stable and consistent measurements), efficient (high output to effort and cost ratio) and precise (low variation between measurements) than the radiocollaring and observation method used in the early 1990s (Person et al. 1996), which we used concurrently with the noninvasive method during 2012–2015 to estimate the POW wolf population. Autumn population sizes were estimated using 1) empirical estimates using an adjusted minimum count; and 2) a territory mapping model that accounted for size of packs and territories (Person et al. 1996, Roffler et al. 2016). The minimum count method does not have an associated measure of precision. The precision of the territory mapping model estimate (CV = 0.432–0.895) was lower than the SECR population density estimate (CV = 0.228–0.365), reducing its utility in detecting changes in the population among years. A further limitation of the territory mapping method was that it was not robust to violations of model assumptions (all available space is occupied by wolf packs, the proportion of wolves in the study area not associated with a pack is consistent; discussed in

Roffler et al. 2016). Counting wolves during aerial telemetry proved to be unreliable because only one-third of the completed flights produced any visual observations of wolves (Roffler et al. 2016). Although data from radiocollared wolves did not prove to be suitable for annual population estimates on Prince of Wales Island, we were able to obtain beneficial information including Global Positioning System location data for assessing seasonal home range sizes, habitat selection, and variation in space use surrounding dens sites (Roffler et al. 2018, Roffler and Gregovich 2018).

Our criteria for evaluation of the noninvasive population estimation method were based on the potential application to long-term monitoring of wolves in densely forested areas. There were several unique challenges encountered while implementing this method in our study area; thus, successful application in other study systems will require careful consideration of these issues. This research represents one of the first attempts to estimate wolf population density using SECR, so further work is required on POW and in other areas for comparison and further method refinement (López-Bao et al. 2018).

Noninvasive methods may be less effective in wet environments; thus, we needed to assess the feasibility of recapturing wolves using DNA from noninvasive samples considering the copious annual precipitation in our study area. Excessive rainfall had been attributed to reduced DNA amplification success using canid scat samples and can result in partial or total removal of the sample from the environment due to the dissolving effect of rain (Morin et al. 2016). Preliminary efforts to initiate this study in 2009–2011 involved attempts to locate wolf scats and amplify DNA for individual genotypes. This effort was not successful because of the low number of fresh wolf scats encountered on road surveys and limited individual genotyping success of degraded samples (D. Person, unpublished data). Rainfall also reduces genotyping success in noninvasive hair samples. For example, Stansbury et al. (2014) demonstrated individual identification success rates using DNA from wolf hair was relatively lower in the wetter section of their study area (71 cm annual precipitation) in comparison to the area that received less precipitation. We took precautions to improve our ability to amplify wolf DNA from hair; we reduced the number of days between hair-snare station checks from 10 days (in 2012) to 7 days and were cautious to air dry samples immediately after collection. Dumond et al. (2015) also found a negative relationship between genotyping success rate using noninvasively sampled bear hair and the number of rainy days between sampling sessions. Therefore, we recommend limiting the interval between sampling sessions to ≤ 7 days in very wet environments, similar to noninvasive DNA sampling-interval recommendations for deer pellets in temperate rainforests (Brinkman et al. 2010).

After initial difficulties in 2012 obtaining enough redetections for a reliable density estimate, we augmented sampling effort by increasing the number of sample occasions, the number of sampling stations, and the total sampling area. These efforts contributed to obtaining sufficient individual redetections during 2013–2015 to

estimate population density. Success of this method was dependent upon obtaining enough spatial redetections; therefore, trap spacing was a key consideration and considered one of the most important design elements in a spatial capture–recapture study (Royle et al. 2014). The ideal study design will balance objectives of obtaining a large number of individuals sampled and a large number of spatial recaptures (Wilton et al. 2014). Resources to conduct fieldwork are finite, so sampling over a larger area translates to lower trap density, which is a scenario that results in more unique individuals captured but fewer spatial recaptures (which causes imprecise and biased density estimates). The reverse scenario (smaller area sampled with greater trap density) results in fewer unique individuals captured, but more spatial recaptures (which causes imprecise density estimates). Results of simulation studies to assess effects of study design on population estimate bias and precision indicate that the optimal trap spacing is $1.5\text{--}2.5 \times \sigma$ (Sollmann et al. 2012, Royle et al. 2014).

The social behavior of wolves contributed to deposition of 13 mixed samples (i.e., hair from >1 wolf) at some of the hair boards in 2013. Mixed samples may have 3 alleles amplify at a locus, and thus have low individual identification genotyping success. Therefore, this is a situation that should be considered, particularly when obtaining a sufficient number of recaptures is challenging because of the scenarios described above. Single-hair catch devices have been implemented in noninvasive monitoring of other species and are useful in eliminating mixing of individual hair samples (Beier et al. 2005, Stricker et al. 2012). However, pilot efforts to develop single-catch hair snares for wolves in southeastern Alaska had limited success in field trials (L. Beier, Alaska Department of Fish and Game, unpublished data). In the absence of a reliable single-catch device, we instead resolved the issue of mixed samples by implementing genotyping screening, wherein hair samples that were suspected to consist of >1 individual were analyzed separately using the single-hair DNA extraction protocol. This procedure resulted in an increased genotyping success rate from 66% in 2012 to 83% in 2013. Photos from trail cameras located at hair board stations did not detect multiple wolves when the samples were deposited in 2014–2015.

Temporal and spatial scales are necessary to consider when using noninvasive spatial capture–recapture methods to estimate large carnivore abundance. One temporal consideration is the seasonal behavior of the study species. We designed the sampling period to coincide with the season of increased mobility of wolves, as pups become large enough to travel in the autumn and less constrained to den and rendezvous sites. When den or rendezvous site locations are known, it is possible to obtain shed hair and scat for individual genetic identification for multiple wolves in a pack including pups (Stenglein et al. 2010, Stansbury et al. 2014). Sampling pups from snared hair obtained from snagging devices is likely more feasible when pups are larger and more mobile. We also considered seasonal attributes of the study system when establishing the sampling design. We expected, as the season progressed into late autumn and early winter,

that fewer bears would be present in the landscape; thus, we could minimize nontarget hair samples or mixed species samples, which do not produce an individual genotype. Despite accounting for seasonal presences of bears, we still obtained 15–25% of bear hair in the samples, although it is probable that summer sampling would result in a larger proportion of bear hair.

The total sampling duration and the number of sampling occasions of a study period is an important design consideration in spatial capture–recapture studies. We designed the time frame of our sampling period to address a need for annual population estimates at the management-unit level, which provide the basis for establishing wolf harvest quotas (based on 20% of the estimated GMU 2 wolf population). We found that within our study system, we collected enough data for a population estimate during a 9–10-week period. However, it is necessary to account for the time required for DNA extraction and individual genotypes to become available for SECR analyses. This process may be time-consuming; so “real-time” population estimates are less possible with noninvasive sampling in comparison to visual surveys of radiocollared animals. Despite this drawback, we were able to provide information for harvest management for the subsequent year (the Federal subsistence wolf hunting season begins in GMU 2 on 1 Sep, and trapping season begins on 15 Nov) by using the population estimates and accounting for known removals (wolves harvested after the sampling was complete).

The ideal total sampling duration of a study period is a trade-off between collecting enough spatial recaptures during the sampling occasions, with an attempt to do so in an abbreviated time period to avoid violations of the assumption of demographic closure. Our study occurred during the beginning of the annual hunting and trapping seasons, so mortalities occurred within our study area during the sample collection period. Known removals of marked animals can be incorporated into the model to eliminate this source of bias, but removals of unmarked animals or unrecorded removals would result in a positive bias in the density and population size estimates. No animals were reported as being taken by hunters or trappers from the study area during the 2014 or 2015 sampling periods; however, 2 known animals were removed during the 2013 study period. Satisfying assumptions of complete demographic closure are difficult in highly mobile species and dynamic populations; therefore, potential approaches to resolve this issue include reducing the sampling period, or planning the sampling period outside of the harvest season, which in GMU 2 extends until 31 March.

Spatial capture–recapture models are able to accommodate a variety of sampling designs at different spatial scales. The extent of the study area is flexible and depends on the study question, biological characteristics of study species (e.g., home range size and movement patterns), and practical considerations such as available resources and access to trap locations. Unlike nonspatial capture–recapture methods, it is not necessary for the trap array to extend over an area many times larger than the average home range of the focal species

(Sollmann et al. 2012). Therefore, spatial capture–recapture is suitable for estimating abundance of wide-ranging carnivores. In practice, the state-space (the region that defines possible values of activity centers) should contain all individuals that may be captured, and the area surrounding the trap array for estimating abundance from density is buffered by $3 \times \sigma$. The study-area extent may vary in size from an area as small as an individual home range to large spatial scales at the landscape level, as long as the main objective of the study design is to sample as many unique individuals in different locations as possible, which will result in more precise parameter estimates (Efford 2004, Sollmann et al. 2012, Royle et al. 2014). Considering the mobility and territoriality of many carnivore species, it is necessary to establish a study area that encompasses the home ranges of many individuals or packs (in the case of social carnivores). Like many management agencies, the ADF&G and the USFS manage wolves at the management-unit level for harvest seasons and bag limits, so it is desirable to estimate abundance at this spatial scale. Other spatial capture–recapture studies have been conducted at broader scales, such as at a regional or provincial level (Morehouse and Boyce 2016, Humm et al. 2017, López-Bao et al. 2018). One option that may enable increasing study area size without increasing the number of traps is cluster sampling, which may help overcome practical limitations such as availability of finite resources, and access to sampling sites (discussed in Royle et al. 2014, Sun et al. 2014).

MANAGEMENT IMPLICATIONS

In GMU 2 wolf populations are managed largely through hunting and trapping regulations (seasons and harvest quotas) based on regulations established by the Alaska Board of Game (for residents and nonresidents) and by the Federal Subsistence Board (for qualified subsistence users on Federal lands). These regulations have been based on a proportion of the total estimated population since 1997 and have ranged from 20 to 30%. Currently, the harvest guideline level is 20% of the autumn population estimate, but it is expected that the Board of Game could raise the harvest limit if the GMU 2 wolf population demonstrably increases. Until this study, there have not been regularly completed wolf population estimates; thus, in the absence of population trend data, harvest decisions have been based on the 1994 population estimate and local knowledge of residents and biologists. In GMU 2, wolf harvest is managed more conservatively than in other parts of Alaska because of conservation concerns of the wolves on Prince of Wales Island. Therefore, regular monitoring of abundance is necessary to ensure the wolf population remains available for sustainable use, as is the mandate of ADF&G. Our results offer an effective method to gain population abundance estimates of widely ranging carnivores at the management-unit level and on an annual basis for regular monitoring and to inform management strategies.

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LITERATURE CITED

- Adams, L. G., R. O. Stephenson, B. W. Dale, R. T. Ahgook, and D. J. Demma. 2008. Population dynamics and harvest characteristics of wolves in the Central Brooks Range, Alaska. *Wildlife Monographs* 170.
- Alaback, P. B. 1982. Dynamics of understory biomass in Sitka spruce-western hemlock forests of Southeast Alaska. *Ecology* 63:1932–1948.
- Albert, D. M., and J. W. Schoen. 2013. Use of historical logging patterns to identify disproportionately logged ecosystems within temperate rainforests of southeastern Alaska. *Conservation Biology* 27:774–784.
- Ausband, D. E., L. N. Rich, E. M. Glenn, M. S. Mitchell, P. Zager, D. A. W. Miller, L. P. Waits, B. B. Ackerman, and C. M. Mack. 2014. Monitoring gray wolf populations using multiple survey methods. *Journal of Wildlife Management* 78:335–346.
- Ausband, D. E., J. Young, B. Fannin, M. S. Mitchell, J. L. Stenglein, L. P. Waits, and J. A. Shivik. 2011. Hair of the dog: obtaining samples from coyotes and wolves noninvasively. *Wildlife Society Bulletin* 35:105–111.
- Ballard, W. B., L. A. Ayres, P. R. Krausman, D. J. Reed, and G. Steven. 1997. Ecology of wolves in relation to a migratory caribou herd in northwest Alaska. *Wildlife Monographs* 135.
- Beier, L. R., S. B. Lewis, R. W. Flynn, G. Pendelton, and T. V. Schumacher. 2005. A single-catch snare to collect brown bear hair for genetic mark-recapture studies. *Wildlife Society Bulletin* 33:766–773.
- Blanco, J. C., and Y. Cortés. 2012. Surveying wolves without snow: a critical review of the methods used in Spain. *Hystrix* 23:35–48.
- Boertje, R. D., C. L. Gardner, M. M. Ellis, T. W. Bentzen, and J. A. Gross. 2017. Demography of an increasing caribou herd with restricted wolf control. *Journal of Wildlife Management* 81:429–448.
- Boitani, L. 2003. Wolf conservation and recovery. Pages 317–340 in L. D. Mech and L. Boitani, editors. *Wolves: behavior, ecology, and conservation*. University of Chicago Press, Chicago, Illinois, USA.
- Borchers, D. L., and M. G. Efford. 2008. Spatially explicit maximum likelihood methods for capture-recapture studies. *Biometrics* 64:377–385.
- Brinkman, T. J., M. K. Schwartz, D. K. Person, K. L. Pilgrim, and K. J. Hundertmark. 2010. Effects of time and rainfall on PCR success using DNA extracted from deer fecal pellets. *Conservation Genetics* 11:1547–1552.
- Burch, J. W., L. G. Adams, E. H. Follmann, and E. A. Rexstad. 2005. Evaluation of wolf density estimation from radiotelemetry data. *Wildlife Society Bulletin* 33:1225–1236.
- Burnham, K. P., and D. R. Anderson. 1998. *Model selection and inference: a practical information-theoretic approach*. Springer-Verlag, New York, New York, USA.
- Duchamp, C., J. Boyer, P. E. Briaudet, Y. Leonard, P. Moris, A. Bataille, T. Dahier, G. Delacour, G. Millisher, C. Miquel, C. Poillot, and E. Marboutin. 2012. A dual frame survey to assess time- and space-related changes of the colonizing wolf population in France. *Hystrix* 23:1–12.
- Dumond, M., J. Boulanger, and D. Paetkau. 2015. The estimation of grizzly bear density through hair-snagging techniques above the tree line. *Wildlife Society Bulletin* 39:390–402.
- Efford, M. 2004. Density estimation in live-trapping studies. *Oikos* 106:598–610.
- Efford, M. G. 2015. secr: spatially explicit capture-recapture models. R package version 2.9.4. <http://CRAN.R-project.org/package=secur>. Accessed 1 May 2015.
- Efford, M. G., D. L. Borchers, and A. E. Byrom. 2009. Density estimation by spatially explicit capture-recapture: likelihood-based methods. Pages 255–269 in D. L. Thomson, E. G. Cooch, and M. J. Conroy, editors. *Modeling demographic processes in marked populations*. Springer, New York, New York, USA.
- Francisco, L. V., A. A. Langston, C. S. Mellersh, C. L. Neal, and E. A. Ostrander. 1996. A class of highly polymorphic tetranucleotide repeats for canine genetic mapping. *Mammalian Genome* 7:359–362.
- Fredholm, M., and A. K. Winterø. 1995. Variation of short tandem repeats within and between species belonging to the Canidae family. *Mammalian Genome* 6:11–18.
- Fuller, T. K. 1989. Population dynamics of wolves in north-central Minnesota. *Wildlife Monographs* 105.
- Gardner, C. L., and N. J. Pamperin. 2014. *Intensive aerial wolf survey operations manual for Interior Alaska*. Alaska Department of Fish and Game, Wildlife Special Publication ADF&G/DWC/WSP-2014-01, Juneau, USA.
- Gasaway, W. C., R. D. Boertje, D. V. Grangaard, D. G. Kelleyhouse, R. O. Stephenson, and D. G. Larsen. 1992. The role of predation in limiting moose at low densities in Alaska and Yukon and implications for conservation. *Wildlife Monographs* 120.
- Gasaway, W. C., R. O. Stephenson, J. L. Davis, P. E. K. Shepherd, and O. E. Burris. 1983. Interrelationships of wolves, prey, and man in interior Alaska. *Wildlife Monographs* 84.
- Hayes, R. D. 1995. Numerical and functional responses of wolves, and regulation of moose in the Yukon. Thesis, Department of Biological Sciences, Simon Fraser University, Vancouver, British Columbia, Canada.
- Hayes, R. D., R. Farnell, R. M. P. Ward, J. Carey, M. Dehn, G. W. Kuzyk, A. M. Baer, C. L. Gardner, and M. O. Donoghue. 2003. Experimental reduction of wolves in the Yukon: ungulate responses and management implications. *Wildlife Monographs* 152.
- Hoelzel, A. R., and A. Green. 1992. Analysis of population-level variation by sequencing PCR-amplified DNA. Pages 159–187 in A. R. Hoelzel, editor. *Molecular genetic analysis of populations: a practical approach*. Oxford University Press, Oxford, England, United Kingdom.
- Humm, J. M., J. W. McCown, B. K. Scheick, and J. D. Clark. 2017. Spatially explicit population estimates for black bears based on cluster sampling. *Journal of Wildlife Management* 81:1187–1201.
- Kendall, K. C., J. B. Stetz, D. A. Roon, L. P. Waits, J. B. Boulanger, and D. Paetkau. 2008. Grizzly bear density in Glacier National Park, Montana. *Journal of Wildlife Management* 72:1693–1705.
- Kery, M., B. Gardner, T. Stoeckle, D. Weber, and J. A. Royle. 2011. Use of spatial capture-recapture modeling and DNA data to estimate densities of elusive animals. *Conservation Biology* 25:356–364.
- Kojola, I., P. Helle, S. Heikkinen, H. Lindén, A. Paasivaara, and M. Wikman. 2014. Tracks in snow and population size estimation: the wolf *Canis lupus* in Finland. *Wildlife Biology* 20:279–284.
- Lake, B. C., J. R. Caikoski, and M. R. Bertram. 2015. Wolf (*Canis lupus*) winter density and territory size in a low biomass moose (*Alces alces*) system. *Arctic* 68:62–68.
- Liberg, O., Å. Aronson, H. Sand, P. Wabakken, E. Maartmann, L. Svensson, and M. Åkesson. 2012. Monitoring wolves in Scandinavia. *Hystrix* 23:29–34.
- López-Bao, J. V., R. Godinho, C. Pacheco, F. J. Lema, E. García, L. Llana, V. Palacios, and J. Jiménez. 2018. Toward reliable population estimates of wolves by combining spatial capture-recapture models and non-invasive DNA monitoring. *Scientific Reports* 8:2177.
- McKelvey, K. S., and M. K. Schwartz. 2005. DROPOUT: a program to identify problem loci and samples for noninvasive genetic samples in a capture-mark-recapture framework. *Molecular Ecology Notes* 5:716–718.
- Morehouse, A. T., and M. S. Boyce. 2016. Grizzly bears without borders: spatially explicit capture recapture in southwestern Alberta. *Journal of Wildlife Management* 80:1152–1166.

- Morin, D. J., M. J. Kelly, and L. P. Waits. 2016. Monitoring coyote population dynamics with fecal DNA and spatial capture–recapture. *Journal of Wildlife Management* 80:824–836.
- Morton, J. M., G. C. White, G. D. Hayward, D. Paetkau, and M. P. Bray. 2016. Estimation of the brown bear population on the Kenai Peninsula, Alaska. *Journal of Wildlife Management* 80:332–346.
- Ostrander, E. A., G. F. Sprague, and J. Rine. 1993. Identification and characterization of dinucleotide repeat (CA) in markers for genetic mapping in dog. *Genomics* 16:207–213.
- Patterson, B. R., N. W. S. Quinn, E. F. Becker, and D. B. Meier. 2004. Estimating wolf densities in forested areas using network sampling of tracks in snow. *Wildlife Society Bulletin* 32:938–947.
- Peakall, R., and P. E. Smouse. 2006. Genalex 6: genetic analysis in Excel. Population genetic software for teaching and research. *Molecular Ecology Notes* 6:288–295.
- Person, D. K., M. Kirchhoff, V. Van Ballenberghe, G. C. Iverson, and E. Grossman. 1996. The Alexander Archipelago wolf: a conservation assessment. U.S. Department of Agriculture Forest Service General Technical Report PNW-GTR-384, Pacific Northwest Research Station, Portland, Oregon, USA.
- Person, D. K., and B. D. Logan. 2012. A spatial analysis of wolf harvest and harvest risk on Prince of Wales and associated islands, Southeast Alaska. Alaska Department of Fish and Game, Final Wildlife Research Report ADF&G/DWC/WRR-2012-06, Juneau, USA.
- Person, D. K., and A. L. Russell. 2008. Correlates of mortality in an exploited wolf population. *Journal of Wildlife Management* 72:1540–1549.
- Peterson, R. O., J. D. Woolington, and T. N. Bailey. 1984. Wolves of the Kenai Peninsula, Alaska. *Wildlife Monographs* 88.
- Pledger, S. 2000. Unified maximum likelihood estimates for closed capture–recapture models using mixtures. *Biometrics* 56:434–442.
- Pritchard, J. K., M. Stephens, and P. Donnelly. 2000. Inference of population structure using multilocus genotype data. *Genetics* 155:945–959.
- Roffler, G. H., and D. P. Gregovich. 2018. Wolf space use during denning season on Prince of Wales Island, Alaska. *Wildlife Biology* 1:wlb.00468.
- Roffler, G. H., D. P. Gregovich, and K. R. Larson. 2018. Resource selection by coastal wolves reveals the seasonal importance of seral forest and suitable prey habitat. *Forest Ecology and Management* 409:190–201.
- Roffler, G. H., J. N. Waite, R. W. Flynn, K. R. Larson, and B. D. Logan. 2016. Wolf population estimation on Prince of Wales Island, Southeast Alaska: a comparison of methods. Alaska Department of Fish and Game, Final Wildlife Research Report ADF&G/DWC/WRR-2016-1, Juneau, USA.
- Royle, J. A., R. B. Chandler, R. Sollmann, and B. Gardner. 2014. Spatial capture–recapture. Academic Press, Oxford, England, United Kingdom.
- Royle, J. A., A. J. Magoun, B. Gardner, P. Valkenburg, and R. E. Lowell. 2011. Density estimation in a wolverine population using spatial capture–recapture models. *Journal of Wildlife Management* 75:604–611.
- Russell, R. E., J. A. Royle, R. Desimone, M. K. Schwartz, V. L. Edwards, K. P. Pilgrim, and K. S. McKelvey. 2012. Estimating abundance of mountain lions from unstructured spatial sampling. *Journal of Wildlife Management* 76:1551–1561.
- Schmidt, J. H., J. W. Burch, and M. C. MacCluskie. 2017. Effects of control on the dynamics of an adjacent protected wolf population in interior Alaska. *Wildlife Monographs* 198.
- Sollmann, R., B. Gardner, and J. L. Belant. 2012. How does spatial study design influence density estimates from spatial capture–recapture models? *PLoS ONE* 7(4):e34575.
- Stansbury, C. R., D. E. Ausband, P. Zager, C. M. Mack, C. R. Miller, M. W. Pennell, and L. P. Waits. 2014. A long-term population monitoring approach for a wide-ranging carnivore: noninvasive genetic sampling of gray wolf rendezvous sites in Idaho, USA. *Journal of Wildlife Management* 78:1040–1049.
- Stenglein, J. L., L. P. Waits, D. E. Ausband, P. Zager, and C. M. Mack. 2010. Efficient, noninvasive genetic sampling for monitoring reintroduced wolves. *Journal of Wildlife Management* 74:1050–1058.
- Stricker, H. K., J. L. Belant, D. E. Beyer, J. Kanefsky, K. T. Scribner, D. R. Etter, and J. Fierke. 2012. Use of modified snares to estimate bobcat abundance. *Wildlife Society Bulletin* 36:257–263.
- Sun, C. C., A. K. Fuller, and J. A. Royle. 2014. Trap configuration and spacing influences parameter estimates in spatial capture–recapture models. *PLoS ONE* 10(10):e0141634.
- U.S. Fish Wildlife Service [USFWS]. 1995. Endangered and threatened wildlife and plants; 12-month finding for a petition to list the Alexander Archipelago wolf as threatened. 60 Federal Register 10056. U.S. Fish Wildlife Service, Anchorage, Alaska, USA.
- U.S. Fish Wildlife Service [USFWS]. 1997. Endangered and threatened wildlife and plants; 12-month finding on a petition to list the Alexander Archipelago wolf as an endangered or threatened species. 62 Federal Register 46709. U.S. Fish Wildlife Service, Anchorage, Alaska, USA.
- U.S. Fish Wildlife Service [USFWS]. 2016. Endangered and threatened wildlife and plants; 12-month finding on a petition to list the Alexander Archipelago wolf as an endangered or threatened species. 81 Federal Register 435. U.S. Fish Wildlife Service, Anchorage, Alaska, USA.
- U.S. Forest Service [USFS]. 1997. Tongass land management plan revision. U.S. Department of Agriculture Forest Service R10-MB-338b. <http://www.fs.usda.gov/detail/tongass/landmanagement/planning/?cid=stelprdb5445359>. Accessed 1 Sep 2015.
- U.S. Forest Service [USFS]. 2008. Tongass land management plan. U.S. Department of Agriculture Forest Service R10-MB-603b, Juneau. https://fs.usda.gov/Internet/FSE_DOCUMENTS/stelprdb5367422.pdf. Accessed 1 Sep 2015.
- Van Oosterhout, C., W. F. Hutchinson, D. P. M. Wills, and P. Shipley. 2004. MICRO-CHECKER: software for identifying and correcting genotyping errors in microsatellite data. *Molecular Ecology Notes* 4:535–538.
- Van Oosterhout, C., D. Weetman, and W. F. Hutchinson. 2006. Estimation and adjustment of microsatellite null alleles in nonequilibrium populations. *Molecular Ecology Notes* 6:255–256.
- Wictim, E., T. Kun, C. Lindquist, J. Malvick, D. Vankan, and B. Sacks. 2013. Developmental validation of DogFiler, a novel multiplex for canine DNA profiling in forensic casework. *Forensic Science International: Genetics* 7:82–91.
- Wilton, C. M., E. E. Puckett, J. Beringer, B. Gardner, L. S. Eggert, and J. L. Belant. 2014. Trap array configuration influences estimates and precision of black bear density and abundance. *PLoS ONE* 9:e111257.
- Wolf Technical Committee. 2017. Interagency wolf habitat management program: recommendations for game management unit 2. Management Bulletin R10-MB-822. U.S. Department of Agriculture Forest Service, U.S. Department of the Interior Fish and Wildlife Service, and Alaska Department of Fish and Game. https://www.fs.usda.gov/Internet/FSE_DOCUMENTS/fseprd537975.pdf. Accessed 13 Jan 2018.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's website.

Table S1. Definition of predictor variables used in spatially explicit capture–recapture (SECR) hybrid mixture models to estimate wolf density, 2013–2015, Prince of Wales Island, Alaska, USA.

Table S2. Number of hair samples successfully identified to the genus level using mtDNA and identified as *Canis* sp., black bears (*Ursus americanus*), marten (*Martes americanus*), nontarget species, or mixed samples, Prince of Wales Island, Alaska, USA, 2012–2015.

Figure S3. Principal coordinate analysis (PCoA) results of pairwise, individual codominant genetic distances using the standardized covariance matrix option to distinguish between wolf (using hair, blood and muscle tissues) and putative dog (using hair) samples. Results were used to visualize genetic clusters based on 10 microsatellite markers. The first and second PCoA axes accounted for 18.38% and 7.95% of the genetic variation, respectively.