

Wolf Population Estimation on Prince of Wales Island, Southeast Alaska: A Comparison of Methods

Gretchen H. Roffler, Jason N. Waite, Rodney W. Flynn, Kristian R. Larson, Brian D. Logan



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Gretchen H. Roffler¹, Jason N. Waite¹, Rodney W. Flynn¹, Kristian R. Larson¹, Brian D. Logan²

¹ Division of Wildlife Conservation
Alaska Department of Fish and Game
PO Box 110024
Juneau, AK 99811

² Tongass National Forest
USDA Forest Service
8510 Mendenhall Loop Rd.
Juneau, AK 99801

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Region I
Division of Wildlife Conservation
Alaska Department of Fish and Game
P.O. Box 100024
Juneau, Alaska 99811



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Cover Photo: This male wolf (number 201501) was captured on Prince of Wales Island during field research in May 2015. ©2015 ADF&G. Photo by Kristian Larson.

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Executive Summary

PURPOSE AND BACKGROUND

This report presents the results of a research project undertaken by the Alaska Department of Fish and Game to evaluate a new method of assessing wolf populations in Southeast Alaska. Estimating population abundance of wolves in Southeast Alaska is challenging because the densely forested landscape obscures visibility and lowers success of traditional methods such as aerial surveys and radio collar mark-recapture. However, regular population estimates of wolves are necessary for sustainable management, particularly in areas where there is elevated concern for the population

In Game Management Unit (GMU) 2, encompassing the Prince of Wales (POW) Island complex, beginning with the 2014–2015 harvest season, the Alaska Department of Fish and Game (ADF&G) reduced wolf harvest from 30 to 20% of the fall estimated population to address concerns of a declining population. During 2015 wolves were considered for listing under the Endangered Species Act (ESA) in Southeast Alaska but were determined to be not warranted for protection (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 Fed. Reg. 435 [published 6 January 2016]).

Until this study, the most recent wolf population estimate for a portion of GMU 2 (POW and Kosciusko Islands = 6,808 km²) was produced for fall 1994 ($\hat{N} = 269$, SE = 80; Person et al. 1996). Because the method used to produce the estimate was costly, it was not repeated in following years. However, regular population estimates at shorter intervals are required for monitoring and managing sustainable populations of wolves; thus refinement of a cost-effective, reliable method is necessary.

Beginning in 2012, ADF&G, in collaboration with the U.S. Forest Service (USFS), initiated a project to address the need for timely and accurate wolf population information. This research is the first attempt to compare methods to estimate wolf abundance in Southeast Alaska and evaluate their effectiveness in terms of cost, effort, and reliability. We used two approaches concurrently within the same northcentral POW study area: 1) population estimates using radiocollared wolf data with the 2 methods previously implemented by Person et al. (1996; empirical estimates using an adjusted minimum count, and a wolf home range model that accounts for size of packs and territories), and 2) capture-recapture using hair samples to identify individuals genetically (noninvasive DNA-based sampling). For the first approach we used foothold traps to capture wolves and instrument them with GPS radio collars. For the second approach we used hair traps to collect DNA samples to estimate fall density using a spatially-explicit capture-recapture approach (SECR; Efford et al. 2004, Borchers and Efford 2008, Kery et al. 2011, Royle et al. 2011). This research represents the first estimate of wolf densities using hair snare and spatial capture-recapture methods.

SUMMARY OF RESULTS

We captured and radiocollared wolves to obtain home range and pack size information explicitly used to estimate the wolf abundance on northcentral POW with the first approach described above. We captured 14 wolves (5 males, 9 females) between May 2012 and June 2015. Twelve of these wolves (5 males, 7 females) were radiocollared. Of these, 3 were juveniles (<1 years old), 3 were yearlings, and 5 were adults (≥ 2 years old) when captured. We monitored the radiocollared wolves 6 June 2012–30 May 2015, during which time we conducted 58 tracking and download flights, and downloaded 16,170 GPS locations. To date, 2 of these wolves are still alive, 9 have died, and the fate of 1 is unknown (the radio collar release mechanism activated as programmed and the collar fell off). Five wolf mortalities were from harvest (4 wolves were trapped and 1 shot), 3 mortalities were attributed to unreported human-caused mortality, and 1 to intraspecific strife.

Mean home range size of wolf packs using minimum convex polygons (MCPs) was 644 km² (range 470–944 km², SD = 261 km) and using adaptive kernel density estimator (KDE) was 454 km² (range 292–644 km², SD = 178). The radiocollared wolves that conformed to a consistent home range throughout our study period represented 2 packs (Honker and Staney), and 1 additional pack (Ratz) that budded from the Honker wolves and occupied an adjacent territory.

The packs monitored during the study ranged from 1 to 16 wolves, with an annual mean of 5.1 (SD = 1.7). The number of packs monitored during fall varied from 3 to 4. Mean pack size in the fall (15 August–31 December) was 6.6 (range 1–16, SD = 1.0), and in the spring (1 March–1 July) was 3.9 (range 1–15, SD = 1.6). Five of the radiocollared wolves were classified as dispersers or extraterritorials during the time they were monitored. Three of the dispersing wolves originated from the Honker pack and dispersed out of the study area, and 1 wolf dispersed into the study area. The extraterritorial wolf overlapped and remained on the periphery of the Staney pack territory both within and outside of the boundaries of the study area throughout the period of time it was monitored.

We assessed wolf reproductive activity to acquire accurate pack size information and monitor wolf pack numbers until fall, when we obtained minimum counts. We accomplished this with ground checks of previously-used den sites, photographic evidence from trail cameras, and aerial observations during radiotracking flights. During the 2012–2015 spring denning seasons, between 1 and 3 active den sites were documented within the study area. The Staney pack produced a litter of 6 pups in 2013. The Honker pack possibly had 2 breeding females with 3 and 7 pups observed at different den sites 8 km apart. During spring 2015 we documented 1 active den site within the Honker home range occupied by 1 wolf pup.

The fall minimum count (the maximum number of wolves observed in the study area) based on known wolf packs was 19 in 2012, 23 in 2013, and 21 in 2014. Expanding these minimum counts (empirical estimates) adjusted upwards by 29% to account for nonresident wolves to the

area of POW and Kosciusko islands (6,808 km²), we obtained fall population estimates for 2012: $\hat{N} = 108$, 2013: $\hat{N} = 131$, and 2014: $\hat{N} = 120$. Because we used minimum counts, we had no measure of variation for the estimate. Thus, we could not calculate a coefficient of variation for these estimates.

Following procedures previously implemented by Person et al. (1996; wolf home range model), we estimated the fall wolf populations for the same area (POW and Kosciusko Islands; 6,808 km²) from the number of known packs, average pack size, and average home ranges (2012: $\hat{N} = 103$, SE = 64, 95% CI = 0–229, CV = 0.63; 2013: $\hat{N} = 163$, SE = 60, 95% CI = 45–281, CV = 0.37; and 2014: $\hat{N} = 143$, SE = 103, 95% CI = 0–345, CV = 0.75). To obtain fall population estimates for POW and Kosciusko islands, we averaged the empirical and home range model estimates (2012: $\hat{N} = 106$; 2013: $\hat{N} = 147$; and 2014: $\hat{N} = 131$). Because the empirical estimates had no variation, we could not calculate a coefficient of variation for these estimates.

Using the second, noninvasive DNA-based hair snare method, the first year of field work in 2012 produced fewer samples than were needed to develop a density estimate. The fall 2013 density estimate was 24.5 ± 6.8 wolves/1,000 km² (95% CI = 14.4–41.9 wolves/1,000 km²; CV = 0.28). Using the fall 2013 density estimate to predict the population in the majority of GMU 2 (9,025 km²) resulted in a population estimate of 221 wolves (95% CI = 130–378). The fall 2014 density estimate was significantly lower than the previous year, determined by bootstrapping a 95% confidence interval for the difference between the two estimates. The density estimate from the top-ranked SECR model was 9.9 ± 3.0 wolves/1,000 km² (95% CI = 5.5–17.7 wolves/1,000 km²; CV = 0.30), and the predicted number of wolves in GMU 2 was 89.0 ± 27.1 (95% CI = 49.8–159.4).

COMPARISON OF POPULATION ESTIMATION METHODS

The 2 population estimation approaches compared in this study both have strengths and weaknesses. As described below, the traditional capture-and-radiocollar approach is costly, imprecise, not statistically robust, and takes more staff time. For monitoring wolf populations in Southeast Alaska, the noninvasive DNA-based approach appears more efficient and economical than the traditional methods. Therefore, the DNA-based approach would be the best approach to use in monitoring efforts requiring repeated estimates. Furthermore, using the noninvasive DNA-based method to estimate the wolf population on POW produces a robust population estimate along with a measure of precision. These features are essential information for sustainable management of wolves. However, a sufficient number of recaptures is required to do this, which we obtained in 2013 and 2014 after increasing the sampling area and intensity.

The traditional capture-and-radiocollar approach can be used to estimate population abundance, home ranges, movement patterns, and demographic rates, but a key requirement is a sufficient sample size of the number of wolf packs and the number of wolves from each pack. However, capturing and radiocollaring wolves in our study environment are labor-intensive and expensive

activities. The heavily timbered landscape requires road-based live-trapping as opposed to aerial-based capture methods. Although this approach was used to estimate the 1994 wolf population estimate in GMU 2, apparent reductions in the wolf population over the last 2 decades make live-trapping less efficient. We have documented an increase in trapping effort required to capture a wolf (0.51 wolves/100 trap nights during 1993–1994 [Person 2001], versus a mean of 0.26 wolves/100 trap nights May 2012–May 2015). For the purposes of population estimates, the approach of live-trapping and radiocollaring wolves was nearly 12 times more expensive than identifying individual wolves genetically and required substantially more trapping effort. In addition, poor visibility hampered observations of associated pack members with radiocollared wolves (i.e., visual observations of wolves occurred in only 33% of the telemetry flights), reducing the effectiveness of this method. Finally, a statistical measure of uncertainty is lacking for the empirical method based on minimum counts. Although standard errors and coefficient of variation could be estimated for the wolf home range model, we found the method to be imprecise and sensitive to violations of model assumptions and therefore not statistically robust. Because of these drawbacks, current population estimates produced using data from radiocollared wolves are not reliable for regular population monitoring in this situation.

IMPROVING THE NONINVASIVE DNA-BASED METHOD FOR MONITORING

We made efforts throughout the project duration to improve the noninvasive DNA-based sampling protocol to make it a more effective tool for wolf monitoring. We did not have a sufficient number of recaptures in the fall of 2012 to reliably estimate wolf population density. Beginning in 2013, we reduced the amount of time between hair board checks (from 10 to 7 days), visibly marked the board sites for weekly relocation, and physically secured them so they could not be moved by the wolves. These efforts contributed to obtaining sufficient individual recaptures in 2013 to estimate population density. We also implemented a genotyping screening protocol, wherein hair samples that were suspected to consist of more than one individual were analyzed separately. This procedure resulted in an increased genotyping success rate from 66% in 2012 to 83% in 2013. Our efforts in 2014 to improve density estimate precision by increasing the hair sampling intensity and sampling area resulted in more wolf hair samples ($n = 108$) than in 2012 ($n = 74$) or 2013 ($n = 86$), and increased the number of unique wolves redetected (2012: $n = 6$, 2013: $n = 8$, 2014: $n = 10$). However, trapping success (detections/trap/100 days) declined in 2014 (0.84 wolves/100 days) in comparison to 2012 (1.32 wolves/100 days) and 2013 (1.88 wolves/100 days). The lower trapping success experienced in 2014 could reflect a variety of conditions, including a reduction in the wolf population in the study area, a redistribution of wolves in the study area (the Staney home range was not occupied by a wolf pack in 2014), changes in wolf behavior, change in study area, or other unknown reasons.

CONCLUSIONS

For estimating wolf population density in an area for either a short time period, or over multiple years as part of a monitoring effort, the results of the noninvasive DNA-based method proved to be more robust, precise, efficient, and cost-effective than the traditional method. In addition to being a method useful for new estimates of the wolf population in GMU 2, the noninvasive DNA-based method has promise for application to wolf monitoring in other regions. The extent of a potential study area is limited mainly by available staffing and access to hair snare locations. Because success of this method is dependent upon obtaining a sufficient number of individual recaptures, it may be necessary to increase the density of nodes, especially in regions where wolf density is believed to be lower than in our study area.

Abstract

Monitoring wolves (*Canis lupus*) in temperate rainforests using traditional radio collar mark-recapture approaches is challenging because of reduced sightability and difficulties obtaining aerial observations. To refine our wolf monitoring strategy, we used 2 approaches concurrently to estimate abundance of wolves in Game Management Unit 2, Alaska, during 2012–2014 based on field data from a portion of the unit. We compared estimation methods for reliability, cost, and effort for application to regionwide monitoring. First, we reproduced a traditional approach that requires capturing and radiocollaring wolves and averaging results from 2 population estimation methods (empirically adjusted fall minimum counts and a previously-developed wolf home range model that accounts for the size of packs and territories). Second, we used hair snares to collect DNA samples in the same northcentral Prince of Wales Island (POW) study area to estimate fall density using a spatially-explicit capture-recapture approach. Fall minimum counts were 19–23 for 2012–2014, but pack size was variable by year. The fall wolf population for POW and Kosciusko Islands using the traditional approach (2012: $\hat{N} = 106$, 2013: $\hat{N} = 147$, 2014: $\hat{N} = 131$) was lower than the previous estimate in fall 1994 using the same method and prediction area ($\hat{N} = 269$, SE = 80). However, direct comparisons of estimates derived using different approaches are problematic. Population density estimates from noninvasive DNA-based sampling were significantly higher in fall 2013 (24.5 wolves/1,000 km², 95% CI = 14.4–41.9 wolves/1,000 km², CV = 0.278) than in fall 2014 (9.9 wolves/1,000 km², 95% CI = 5.5–17.7/1,000 km², CV = 0.304). The predicted fall population for the majority of GMU 2 (9,025 km²) using density estimates was 221 wolves (95% CI = 130–378) for 2013 and 89 wolves (95% CI = 49.8–159.4) for 2014. Our efforts in 2014 to improve density estimate precision by increasing the hair sampling intensity and area resulted in more wolf hair detections and redetections, and increased the number of unique wolves redetected. A change in study area size between years muddles comparison of density across years, but demonstrates the value of increased sampling effort. Comparing the 2 approaches with the end goal of producing population estimates, live-trapping and radiocollaring wolves were nearly 12 times more expensive than identifying individual wolves genetically, and required more trapping effort. Moreover, a statistical measure of uncertainty is lacking for the empirical method based on minimum counts, and although standard errors could be estimated for the wolf home range model, we found the method to be imprecise and sensitive to violations of model assumptions. Both the traditional and noninvasive DNA-based methods have strengths and weaknesses, but for monitoring wolf populations in Southeast Alaska, the latter can be more feasibly and economically applied, and produces a more statistically robust population estimate.

Key words: *Canis lupus*, home range, noninvasive, population estimation, SECR, spatially-explicit capture-recapture, wolves

Introduction

Wolves (*Canis lupus*) in the temperate rainforests of Southeast Alaska are cryptic, rendering traditional methods of population estimation such as aerial surveys and radiocollar mark-recapture challenging. Conservation concerns have been elevated for wolves in Southeast Alaska and the U.S. Fish and Wildlife Service (USFWS) has twice conducted a 12-month Endangered Species Act (ESA) review in the past 20 years (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 Fed. Reg. 46709435 [published 4 September 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. 81 Fed. Reg. 435 [published 6 January 2016]). The wolf is also a management indicator species within the Tongass National Forest Land and Resource Management Plan (USFS 1997, USFS 2008). The complexities of managing wolves, deer, forests, roads, and human use of these resources in a managed landscape underscore the need for timely population estimates. In a move towards more conservative wolf management in Game Management Unit (GMU) 2, encompassing the Prince of Wales (POW) Island complex, the Alaska Department of Fish and Game (ADF&G) limited the 2014–2015 harvest of wolves at 20% of the fall population estimate, a reduction from the previous 30% limit. Refinement of a cost-effective, reliable method is necessary for monitoring and managing sustainable populations of wolves. Until fall 2013, the most recent population estimate for GMU 2 wolves had been produced for the fall of 1994 (Person et al. 1996). Considering the concerns regarding GMU 2 wolves in the context of wildlife and forest management, regular population estimates are required for effective management.

Beginning in 2012, ADF&G, in collaboration with the U.S. Forest Service (USFS) initiated a project to address the need for timely and accurate wolf population information. During 1992–1995 and 1999–2004, wolves were captured and radiocollared in the northcentral portion of POW, and population abundance was estimated for fall 1994 and spring 1995 using radiocollared wolves to locate packs and aurally count the pack members. Obtaining the large sample size of marked wolves required for this method can present a challenge. This is especially the case when using foothold traps on a wolf population with substantial harvest levels. The reason is twofold: heavy harvest can reduce wolf abundance and corresponding frequency of wolf travel through trapping areas, and wolves that escape traps have learned to avoid them. Counting wolf pack numbers is also hindered by the dense forest canopy in the temperate rainforests of this region. To address these drawbacks, we sought to rigorously test an alternate population estimation technique that could be applied in this environment. Genetic capture-recapture from hair has been used to estimate population abundance of cryptic species living in dense forests (Kendall et al. 2008, Morton et al. 2015), including wolves (Stenglein et al. 2010, Ausband et al. 2011, Ausband et al. 2014, Stansbury et al. 2014). The development of spatially-explicit capture-recapture techniques (SECR; Efford et al. 2004) has provided a means to estimate animal density by incorporating spatial information from locations of animal captures and movements.

Successful application of SECR requires multiple recaptures of the same wolves in different locations. Thus, we needed a thorough assessment of our ability to detect and redetect individual wolves from noninvasive samples.

The primary objective of this project was to develop and refine a protocol to estimate wolf population abundance in densely forested regions. We applied 2 population estimation approaches concurrently within the same study area: 1) using foothold traps we captured and radiocollared wolves then used tracking data to produce population estimates with the 2 methods previously implemented by Person et al. (1996; empirical estimates using an adjusted minimum count, and a wolf home range model that accounts for size of packs and territories), and 2) capture-recapture using hair samples to identify individuals genetically (noninvasive sampling). We implemented the 2 approaches independently, and determined consistency in results between population estimates. As part of the original study plan for this project a third method (surveys of harvesters to document perceived trends in wolf abundance and harvester activity) was evaluated. The results of this work are documented and discussed separately (Sill 2014). Although our monitoring efforts focused on the northcentral region of POW, the intent was to develop a monitoring strategy that could be used routinely with the appropriate sampling frame to monitor wolf populations in GMU 2 and other regions throughout Southeast Alaska in the future. Thus, our secondary objective was to assess the effectiveness of these 2 approaches in terms of cost, effort, reliability, and appropriate spatial scale for application to region-wide monitoring. Tertiary objectives related to the previously-used population estimation approach (1, above) included monitoring reproductive activity and wolf pack size, and estimating home range sizes and configuration. This research represents the first estimate of wolf densities using hair snare and spatial capture-recapture methods.

Study Area

The POW Island complex is located in the southern portion of the Southeast Alaska Archipelago (Fig. 1) and is characterized as a temperate rain forest ecosystem. This land mass is defined by an extensive coastline with long fjords, and contains rugged mountains $\leq 1,160$ m, watersheds, and large tracts of forests. Sitka spruce (*Picea sitchensis*) and western hemlock (*Tsuga heterophylla*) are dominant at elevations below 600 m (Alaback 1982), and other habitats including muskegs, riparian, and alpine areas are represented to a lesser extent. Old-growth forest is interspersed with a patchwork of even-aged forest stands at different successional stages resulting from clearcut logging. Annual precipitation ranges between 130 and 400 cm mostly in the form of rain, with intermittent snow during the winter months that occasionally accumulates >50 cm (Shanley et al. 2015). The human population increased during 1950–1990 coinciding with growth of the logging industry, and the current population of 3,500 is distributed among 11 communities (Brinkman et al. 2009). Compared to other regions in Southeast Alaska, northern POW has the highest rates of logging, where contiguous high-volume forests have been reduced by 93.8% between 1954 and 2004 (Albert and Shoen 2013). To facilitate logging, approximately

6,800 km of roads have been built throughout POW, with the highest road densities in northern POW (0.49–1.04 km/km²; Person and Russell 2008, Person and Logan 2010), comparatively higher than road densities in other areas of Southeast Alaska. Prior to this study, high levels of wolf harvest (1.7–14.3 wolves/1,000 km², 2000–2009; Person and Logan 2010) have occurred on northern POW relative to other regions in GMU 2.

During 2012–2013, the wolf capture and hair collection study area covered 1,683 km² in the northcentral portion of POW, representing ~20% of GMU 2 (Fig. 1). Previous wolf research conducted in this same geographical area documented 8 wolf packs, constituting approximately 25% of the estimated population for GMU 2 (Person 2001). Since monitoring was reinstated in 2012, this area has encompassed 2–3 wolf pack home ranges. In an attempt to better understand the spatial variability of wolf population dynamics, we expanded the study area during fall of 2014 (Fig. 1). We increased the area of live-captures to 2,899 km² (representing 32% of GMU 2) by expanding our efforts to the northern end of POW and to the south of the traditional study area (Fig. 1a). We also increased the extent of our noninvasive DNA-based sampling area to 3,281 km² in 2014 (Fig. 1b), which represents about 36% of GMU 2.

Methods

CAPTURING AND RADIOCOLLARING WOLVES

Captures

Capture efforts occurred over approximately 4 weeks in spring (late May–late June 2012, and late April–late May 2013–2015) and 6 weeks in early fall (mid-September–late October 2012–2014). We used a combination of padded long spring (Easy-Grip® #7, Livestock Protection Company, Alpine, TX) and unpadded coil spring foothold traps (MB750, Minnesota Brand Inc.). We modified these traps to have an increased offset (1.3–1.5 cm) and smoothed the jaws of MB750 traps to prevent cutting the wolf's foot. We buried the traps along the USFS road system with commercially-produced lures and canid urine used as attractants. Between 26 and 103 sets were simultaneously deployed during the 7 trapping sessions. We used ATS (Isanti, MN) motion-detecting (model M4010B) and Telonics (Mesa, AZ) magnet-activated trap transmitters on a subset of the sets to determine when a trap had been disturbed. We calculated the total number of trap nights as the time period when traps were functional and lured. Traps were given the value of 0.5 trap nights if they were not functional because they were closed or missing, or if the trap captured an animal (Beauvais and Buskirk 1999). Trapping effort was standardized as the number of catches per 100 trap nights.

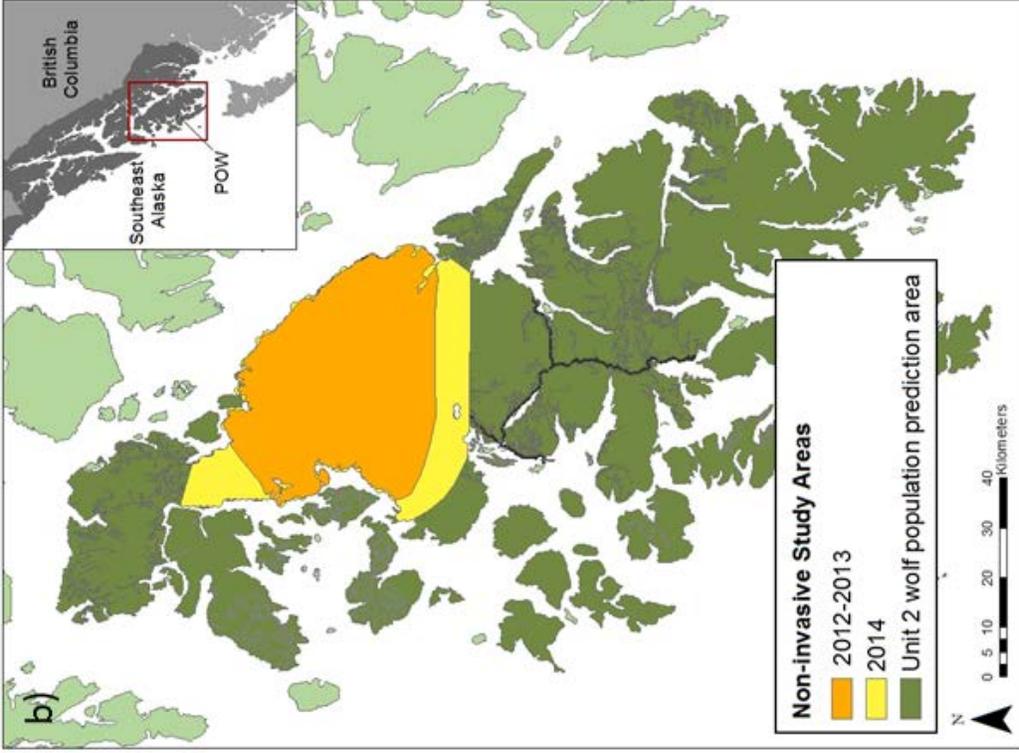
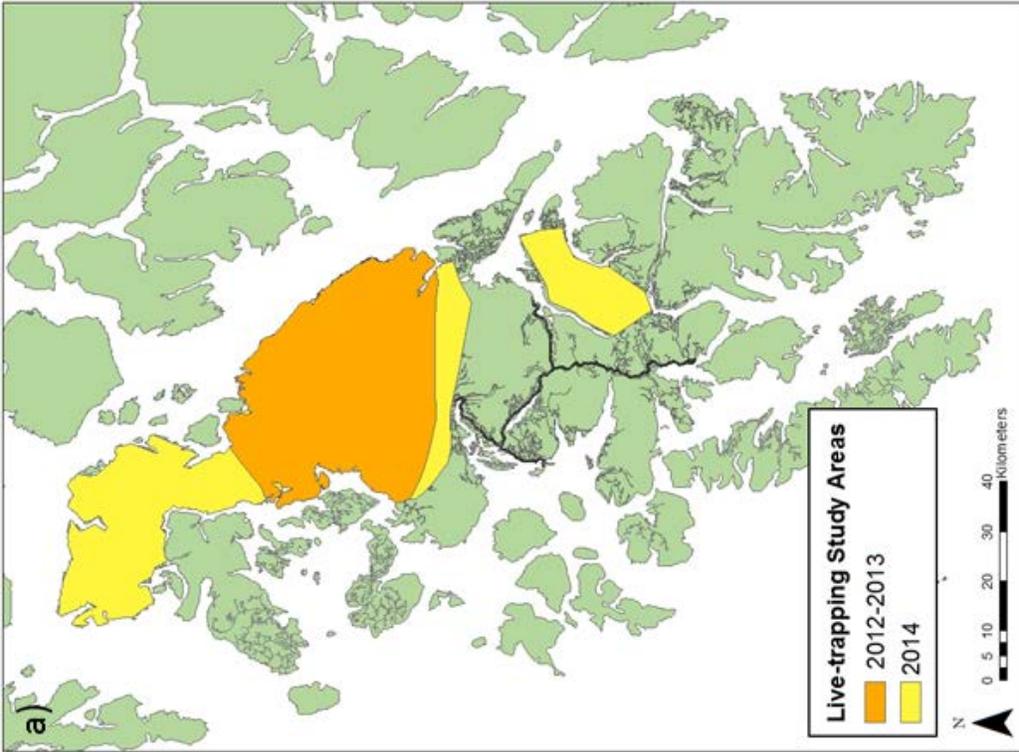


Figure 1. Study areas for a) wolf live-trapping, and b) noninvasive DNA-based sampling (hair boards) with 10-km buffer, Prince of Wales Island, Alaska, 2012–2015.

Restraigned wolves were immobilized using either tiletamine HCl and zolazepam HCl (Telazol®; Fort Dodge Animal Health, Ford Dodge, IA; 229 mg/ml concentration, 3–10 mg/kg), or a combination of ketamine (Fort Dodge Animal Health, Ford Dodge, IA; 200 mg/ml concentration, 4–6 mg/kg) and medetomidine (Domitor ®; Pfizer Animal Health, New York, NY; 20 mg/ml concentration, 0.08–0.15 mg/kg). Immobilization drugs were administered with a jab pole. We recorded sex, morphological data, and age category for each wolf (juvenile, <1 year; yearling, ≥1 and <2 years; and adult, ≥2 years), which was determined by palpating the epiphyseal process on the front legs (Rausch 1967). We also collected blood, hair, and ear punch skin tissue. Each captured wolf was fitted with a spread-spectrum, Global Positioning System (GPS) radio collar (Mod 4500, Telonics, Inc.) programmed to obtain a location every 6 hours during 1 January–31 August, and every 2 hours 1 September–31 December. Collars were programmed to automatically release after 24 months. We affixed ear tags to wolves captured during fall 2014 and afterward for individual identification. Capture and handling procedures conformed to guidelines established by the ADF&G Animal Care and Use Committee (ACUC #2012–028 and #2014–15) and the American Society of Mammalogists (Sikes and Gannon 2011).

RADIOTRACKING FLIGHTS

Using a fixed-wing airplane (Cessna 185) equipped with a receiver antenna, we aerially tracked radiocollared wolves and remotely downloaded collar location data approximately every 2 weeks. We attempted to obtain a visual observation of marked wolves, along with their pack members, to count the minimum number of wolves per pack. When mortalities were detected, they were immediately investigated and carcasses were retrieved and necropsied when possible.

HOME RANGE ESTIMATES

We used radio collar GPS location data to determine home range size and geographic extent of wolf packs. Home ranges were based on GPS locations during the biological year (1 May–30 April) to reflect birth of pups in early May (Mech et al. 1998) and included 2 years of location data when possible to ensure adequate sample size (Burch et al. 2005). We also estimated annual home ranges for use in annual population estimates. We used minimum convex polygons (MCP; Mohr 1947, Burch et al 2005) and 95% adaptive kernel density estimators (KDE; Worton 1989) to estimate home ranges for packs. Home range estimation included data from all radiocollared wolves belonging to a pack and excluded obvious dispersal events or extraterritorial forays (Ballard et al. 1997, Burch et al 2005), defined as locations separated by ≥15 km from the centroid of the pack (geographic center [mean latitude, longitude coordinates]). We quantified MCPs using the Geospatial Modeling Environment (GME; Beyer 2012) and KDEs using a fixed bivariate Gaussian kernel model (smoothing factor href = 100, cell size = 100) using ArcMET software (Wall 2014).

Following Person (2001), and based on GPS location data of individual wolves in relation to other marked wolves and existing wolf pack home range territories, we classified wolves into residents, extraterritorials, and dispersers. Resident wolves were associated with other wolves in the pack home range and did not permanently leave the pack territory during the time they were monitored (Ballard et al. 1997). Extraterritorial wolves and dispersers are referred to here collectively as nonresident wolves (*sensu* Person 2001). Extraterritorial wolves have been recognized in other studies and individuals are categorized as such when their spatial locations are markedly separate from their previous locations (Ballard et al. 1987, Fuller 1989, Burch et al. 2005, Adams et al. 2008), although specified distances vary among studies. These movements outside of regular home range patterns may be the result of temporary forays (Ballard et al. 1997), or precede establishment of home ranges on the edge of, or overlapping with, other wolf pack home ranges (Person 2001). Extraterritorial movements may also precipitate dispersal (Mech and Boitani 2003), defined as a permanent movement away from the resident home range to a nonadjacent area (Ballard et al. 1997), but remaining within a population (Adams et al. 2008). Dispersal is differentiated from extraterritorial forays as generally being permanent as opposed to temporary, and by the succession of frequent movements, and as defined by Person and Russell (2008) not remaining in one location for >14 days. Individual wolves may cycle through these different classes throughout the course of their lifetime (Mech and Boitani 2003, Person and Russell 2008) sometimes in short succession.

TRAIL CAMERAS

We deployed remotely triggered motion-detecting cameras (Reconyx HC600, Reconyx, Inc. Holmen, WI, or Moultrie M990i, Moultrie Products, Alabaster, AL) to record activity at a subset of the hair-trap stations, at known den sites, and in suspected travel corridors. The cameras had motion-sensing and infrared technology, and could detect animals at up to 15 m away. Cameras were programmed to operate 24 hours a day, to take a burst of 3 photos every 5 seconds when triggered, and to record date, time, temperature, and camera ID on each photo.

REPRODUCTION

Wolf reproductive activity was assessed using 3 methods. First, we conducted ground checks of previously-used den sites that had been identified during 1993–2004 (Person and Russell 2009). We also investigated suspected den sites based on GPS locations of adult females and habitat characteristics within areas of observed use during April–May (Person and Russell 2009). Second, we used photographic evidence from trail cameras established at active den sites, or locations nearby, through fall (wolf pups are distinguishable from adults until 6 months old). Third, we recorded the number of pups observed in a wolf pack during radiotracking flights.

MINIMUM COUNTS

To estimate fall (15 August–31 December) minimum counts of wolves, we quantified wolves observed while monitoring radiocollared wolves by aerial telemetry (Fig. 2) and those seen in photos collected from trail cameras (Fig. 3). The maximum number of wolves observed was considered to be the minimum wolf population known to be alive during fall. We used the same study area as the noninvasive DNA-based method (1,683 km²) because our efforts to produce a minimum count are comparable to the noninvasive DNA-based effort during this time.

POPULATION ESTIMATION FROM RADIOCOLLAR DATA

Person et al. (1996) estimated 1994 population size based first on the minimum count (empirical estimate) for the northcentral POW study area (1,683 km²). Next, they adjusted their estimate by 29% to account for the proportion of nonresident wolves they had determined was in the population. They then used population density estimates for the study area to predict the population for the larger area of POW and Kosciusko Islands (6,808 km²). We used similar methods to estimate wolf populations for comparative purposes. Because we used minimum counts and had no measure of variation for our estimate, we could not calculate a coefficient of variation for these estimates for comparisons with population estimates that had a measure of uncertainty, such as those produced using the wolf home range model and noninvasive DNA-based sampling (described below).



Figure 2. Aerial photograph of wolves during a radiotracking flight, September 2012. We used the wolves observed on the radiotracking flight for our minimum counts of pack members.



Figure 3. Photograph of wolves from a trail camera, December 2013. We used photographs from trail cameras for our minimum counts.

The number of known packs, pack size, and home ranges were used to derive a population estimate (Person et al. 1996), as follows (henceforth the “wolf home range model”):

$$W_{\text{pop}} = \frac{A}{HR/1 - \alpha} * \frac{W_{\text{pack}}}{(1 - \beta)}$$

eq. 1

Where A is the total area of the population estimate, HR is the average home range size (calculated as the mean of the MCP and the 95% KDE home ranges), α is the proportion of home range overlapping adjacent home ranges, W_{pack} is the average number of wolves per pack, and β is the proportion of nonresident wolves (dispersers and extraterritorials) in the population (29% based on empirical radiocollar data collected 1992–1995; Person et al. 1996, Person 2001). The proportion of nonresident wolves in a population can vary over time and is influenced by the age structure of the population, but long-term means across North American wolf populations are 10–40% (Fuller et al. 2003). We used the previously-estimated proportion of nonresidents because it falls within this range and reflects a greater sample size of the population than our current study. We used the delta method implemented in the R package “car” (Fox and Weisberg 2011) to estimate standard error of the population estimate, and then we calculated coefficients of variation for each estimate to evaluate different sampling approaches.

Person et al. (1996) averaged these 2 population estimates (empirical and wolf home range model estimates) ($\bar{N} = 269$) because they believed the wolf home range model overestimated the fall wolf population ($\hat{N} = 321$) as not all available land was likely permanently occupied by wolf packs throughout GMU 2, and the empirical estimate ($\hat{N} = 218$) underestimated the wolf population because of heavy harvest in the study area for the years preceding the fall 1994 population estimate. We duplicated these methods for comparison of the 1994 and our current population estimates. Because the empirical estimates had no measure of variation, we could not calculate a coefficient of variation for these combined estimates.

NONINVASIVE DNA-BASED POPULATION ESTIMATION

Array Design

During fall 2012–2014, we established an array of hair-trap (hereafter hair board) nodes across the study area to estimate the density of wolves. We increased node density and extent in 2014 with the intention of obtaining more hair samples and improving the precision of our population estimates. The average distance between the nodes was roughly 3.9 ± 1.1 km during 2012–2013 and 3.5 ± 1 km during 2014. Nodes consisted of 5 hair boards set within 100-m spacing intervals. Hair board nodes were deployed 20 October–30 December (2012, $n = 37$; 2013, $n = 36$; 2014, $n = 72$; Fig. 4).

Sample Collections

A behavioral response of canids is to scratch and rub at a scent mark (Ausband et al. 2011). We applied lure to the hair boards to evoke this response which enabled us to collect wolf hair noninvasively to extract DNA for individual identification through genotyping. In a design modified from Ausband et al. (2011), we constructed the hair boards from 23×15 cm pieces of plywood and mounted them with 3 parallel strips of #14 four-prong barbed wire (Fig. 5). We used 16 gauge tie wire in 2 attachment points for each strand of barbed wire, threaded through holes drilled in the board, and wrapped with the twisted ends on top to provide more features for snagging hair. To stabilize the boards and prevent wolves from moving them, 16 penny nails were driven through holes drilled into each corner of the board and into the ground, and the boards were affixed with a length of wire and tied off to a flagged tree or branch. Hair boards were set just beneath the level of the substrate and lightly covered with dirt or moss to provide camouflage. Each board was doused with ~5 ml of commercially produced lure.

We checked hair board nodes every 10 days in 2012, and every 7 days in 2013–2014. We reduced the length of time between node checks to minimize genotyping error due to exposure of hair follicles to moisture, and to obtain more hair samples to increase our chances of detecting recaptures. If hair was present on the board, it was collected using sterilized tweezers or needle nose pliers, stored in labeled coin envelopes, and allowed to dry.

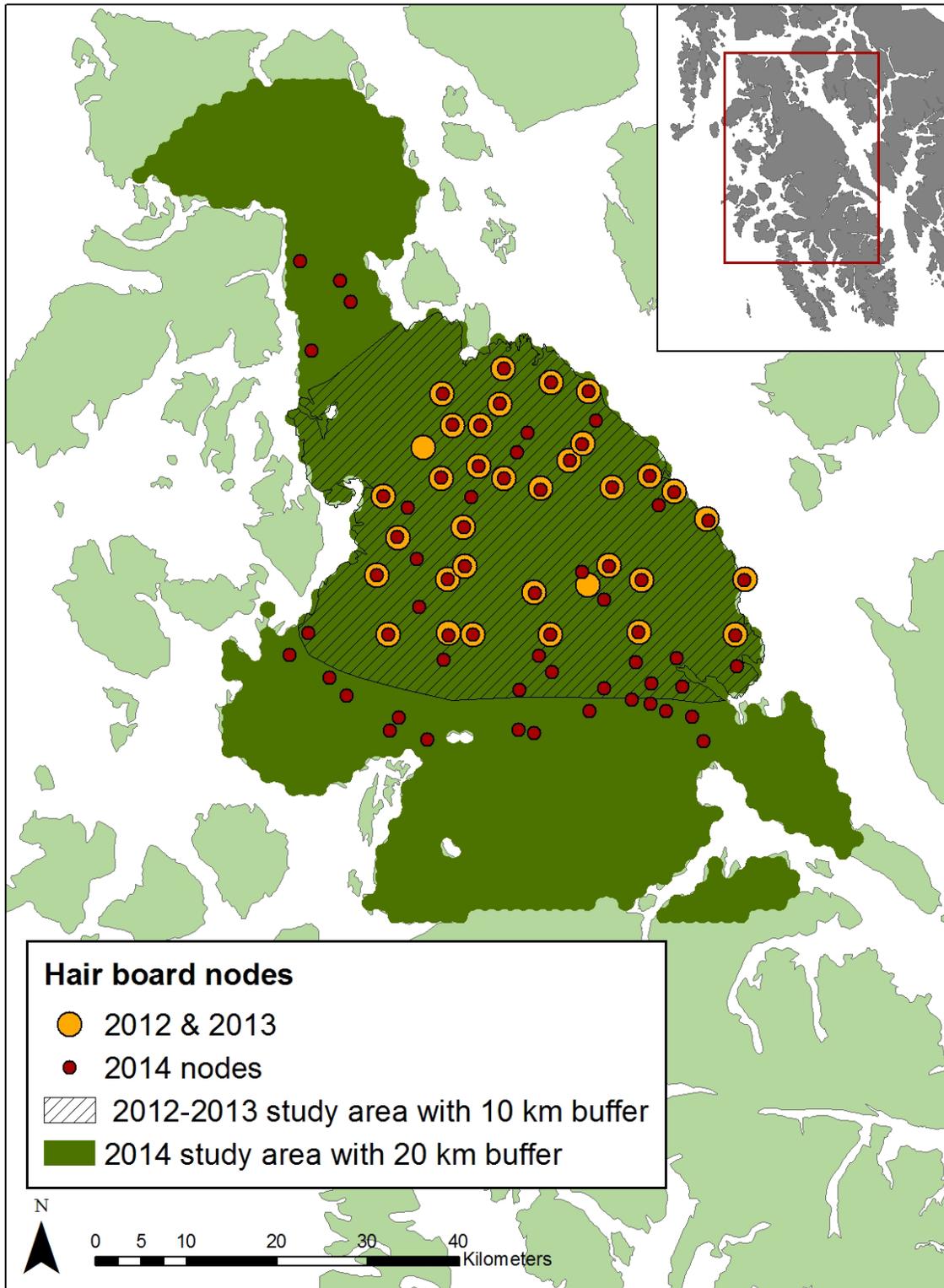


Figure 4. Hair board nodes deployed 20 October–30 December 2012–2014 and the SECR analysis area with a 10-km (2012–2013) buffer and 20-km (2014) buffer around the trap array, Prince of Wales Island, Alaska. The 2012–2013 and 2014 SECR study areas equate to 1,683 km² and 3,281 km², respectively.



Figure 5. Photograph of a hair board, October 2014. We used these boards to collect wolf hair. We extracted DNA from the hair follicles for identification of individual wolves on our study area, Southeast Alaska.

The boards were then burned clean of remaining hair fragments using a soldering torch. Lure was reapplied each session regardless of whether hair was present or not. We collected 64 hair samples in 2012, 93 in 2013, and 137 in 2014.

We also obtained muscle samples from, and harvest locations of, wolves taken during the annual 1 December–31 March hunting and trapping seasons (State of Alaska regulations; ADF&G 2014), the 1 September–31 March Federal subsistence hunting season, and the 14 November–31 March Federal subsistence trapping season. We collected 40 muscle samples in 2012, 49 in 2013, and 29 in 2014. Finally, we collected muscle samples from one road-kill wolf, and from one wolf killed by an unreported human-caused event, in addition to blood samples from 10 of the wolves captured during this project for radiocollaring.

Genotyping

DNA extractions, genetic identification of species, and wolf genotyping were conducted at the USFS Rocky Mountain Research Station in Missoula, MT. Whole genomic DNA was extracted from hair and muscle samples using standard protocols for tissues (DNeasy Tissue kit; Qiagen, Valencia, CA) with overnight incubation in lysis buffer and Proteinase K on a rocker at 60°C. Samples were identified to the species level using the mitochondrial DNA (mtDNA) control region. The control region analysis does not distinguish between wolves and dogs (*Canis familiaris*), thus we used principal coordinate analysis (PCoA) to visualize clustering and

distinguish between these groups with microsatellite data (GenAlEx 6.5; Peakall and Smouse 2006). We evaluated DNA from blood and muscle tissue from radiocollared and harvested wolves from GMU 2 using a suite of microsatellite DNA markers used previously on other wolf studies. Ten loci were variable in our wolf population and also amplified consistently in noninvasively collected DNA samples: cph5 (Fredholm and Wintero 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 theoretical probability that 2 random individuals ($P_{(ID)}$) have the same genotype using GenAlEx 6.5. The 10 variable microsatellite loci produced a cumulative $P_{(ID)} = 4.35 \times 10^{-7}$, providing acceptable power to identify individuals from the noninvasive samples.

Using samples identified as “canids,” we performed genotyping for individual identification with the 10 microsatellite DNA markers. To minimize genotyping errors, we reanalyzed the same samples multiple times to obtain a consensus genotype. We accepted data from the hair samples only if the microsatellites produced consistent scores in 2–4 PCR amplifications. We used DROPOUT (McKelvey and Schwartz 2005) to estimate and efficiently eliminate genotyping errors, and estimated the genotyping error rate as the proportion of the successful PCRs that amplify DNA. We also estimated the proportion of all PCRs yielding the correct consensus genotype. We targeted 10 good hairs (with follicles) for the extraction, except in situations when we had evidence of more than 1 individual wolf depositing hair on the same board (from cameras, or from very large clumps of hair collected on a board). In these cases, we implemented a single hair protocol to detect multiple individuals from these samples and eliminate the chance for mixed hair samples, which would increase error in consensus genotyping. This protocol consisted of selecting the 4 best hairs (with follicles) from different locations in the hair clump, and performing DNA extractions on each hair. Sex of individual wolves was identified using the canid SRY marker (Wictum et al. 2013).

Population Density Estimates

We used SECR models (Efford 2004, Borchers and Efford 2008) to estimate the density and population size of wolves in our study area. SECR is a set of mark-recapture methods used to estimate animal density by incorporating the detection histories of individual animals with information on the spatial locations of the detectors (traps, hair snares, cameras, etc.) and of the actual detections. These data, together referred to as 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), which relates the probability of detecting an animal given the distance between its activity center and the detector. Unlike traditional capture-recapture methods that rely on a study area that is somewhat arbitrarily defined *post hoc*, SECR models explicitly link the density estimate to a specific, predefined landscape and the resulting density estimates are not affected by edge effects (Borchers and Efford 2008).

Spatial detection histories based on multiple sampling occasions were compiled for wolves that had been uniquely identified from DNA extracted from hair deposited on the hair boards. A sampling occasion was defined as the period between checks of all nodes in the study area and the length of a sampling occasion was allowed to vary for each node individually based on actual node exposure time. If a node was not checked during a given areawide sampling occasion due to severe weather or snow conditions, that node was considered to be inactive for that occasion, but the length of the subsequent node-specific occasion was then increased to account for the actual number of days the node was active (exposure time). For example, if a node was not checked (but was deployed) after the first 7-day sampling occasion, it was assigned an exposure time of 0 days for that occasion. However, if that node was then checked after the second 7-day sampling occasion, it was considered active for that occasion and assigned an exposure time of 14 days. This allowed the actual exposure time to be taken into account while acknowledging the uncertainty as to the specific occasion a sample was deposited. We also considered trap usage based on binary occasion lengths (1 = active, 0 = inactive), but as exposure times were relatively homogenous over the duration of the study period and missed node checks relatively rare, parameter estimates were not substantially affected.

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 also examined the effects of collapsing detections of an animal at individual hair boards within a node to a single detection event and determined that density estimates were not affected. We specified “count” type detectors in the SECR model, which allows for 1) detections of multiple animals at same detector during the same occasion (i.e., the detectors do not fill up and become unavailable to other animals after the first detection event), and 2) detections of the same animal at multiple locations during the same occasion (i.e., animal movement was not restricted by the detector following a detection event).

A discrete habitat mask based on a 500-m grid was defined for the study area by delineating a 10-km buffer (in 2012 and 2013) or a 20-km buffer (in 2014) around the trap array, and then clipping to the POW shoreline (Fig. 4). The resulting study areas encompassed an area of 1,683 km² in 2012–2013, and 3,281 km² in 2014. The size of the buffer was selected based primarily on the maximum extent of animal movement during the study period and was selected to minimize the probability of detecting an animal in the trap array whose activity center was located outside of the study area. Note that the size of the buffer is not intended to encompass the home ranges of all animals in the study area or to constrain animals from temporary movement into or out of the study area.

We incorporated binary covariates, such as sex, (Appendix A) by fitting hybrid mixture models to the data (Pledger 2000). Hybrid mixture models allow for missing covariate values, but when covariate values are known for all detected individuals, these models are identical to the full likelihood specification but with the added benefit of a mixture term to estimate the proportion of the total population belonging to each group (e.g., population sex ratio). We evaluated a suite of

competing models that included a variety of biologically-plausible coefficients on detection probability and space usage. In addition to sex, we examined the effects of various behavioral responses and site-specific changes in effectiveness on detection probability and movement parameters. Model selection was based on information theoretic methods (Burnham and Anderson 1998).

We used wolf density estimates from the study area to predict the GMU 2 (9,025 km²) wolf abundance, making the explicit assumption that mean wolf density in the study area would be representative of the mean wolf density across GMU 2. Estimating the population at the GMU level is useful because wolf harvest is managed at this spatial scale by ADF&G. Like many predictions of a density estimate from a study area to a larger area, a number of untested assumptions are inherent in the approach; nevertheless, this occurs commonly in wolf population estimations specifically (Boitani 2003) and in wildlife studies in general where there is a need to make management decisions across an area larger than a research study area.

We assessed significant differences 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. Analyses were conducted using R version 3.1.1 (R Development Core Team 2014) and the package SECR version 2.9.4 (Efford 2015). All parameter estimates are presented \pm 1 SE unless otherwise indicated. Home range estimates, wolf pack sizes, and distances between sequential recaptures are presented as mean \pm SD.

Results

CAPTURES AND RADIOCOLLARED WOLVES

Captures

We captured and radiocollared 12 wolves between spring 2012 and spring 2015, including 5 males and 7 females (Fig. 6, Table 1, Appendix B). In addition, 2 wolves were captured that were not radiocollared: a female juvenile was captured during spring 2012 that was too small to be radiocollared, and an adult female captured during spring 2015 that died of aspiration pneumonitis during handling. Of the radiocollared wolves, 5 were adults when captured, 4 were yearlings, and 3 juveniles (Table 1).

We monitored traps for a total of approximately 9,950 trap nights during May 2012–May 2015. With the exception of spring 2013 when no wolves were captured, trap success ranged from 0.04 to 0.76 wolves captured per 100 trap nights (Table 2). Trapping success was higher during the spring (mean = 0.33) than during the fall (mean = 0.10). On average, 829 trap nights were required to capture a wolf, and the average rate of capture was 1 wolf per 20 nights. For this project it cost on average \$28,791 to capture, radiocollar, and monitor each wolf (Table 3).

Radiotracking Flights

We monitored radiocollared wolves during 6 June 2012–30 June 2015 (Table 4, Appendix B). We conducted 58 tracking and download flights of the 12 radiocollared wolves and downloaded 16,170 GPS locations for analyses of pack home range size and movement patterns.

WOLF FATES

Wolves were monitored on average 328 days (SD = 220). Of the 12 radiocollared wolves, 9 died, 2 were alive as of 30 May 2015, and the fate of 1 is unknown (the radio collar release mechanism detonated as programmed; Table 4, Appendix B). Of the known mortalities, 4 wolves were trapped and 1 was shot during the harvest season. Three wolf mortalities were attributed to unreported human-caused mortality. Wolf AF430 died during the trapping season and was found in late March 2013 near a wolf set with wounds consistent with leg-hold trap injuries, and AM260 died from gunshot wounds in September 2013. Wolf AM310 dispersed in January or February 2013 and was not relocated until its remains were discovered in July 2015. The suspected cause of death was from wounds sustained from a snare, and the approximate date of mortality was during the winter of 2013–2014. The 3 unreported human-caused mortalities were located by tracking the radio collars, which were emitting mortality signals and were still affixed to the wolves. Finally, during late fall, 1 wolf from the Honker pack dispersed to the southern end of the island and was killed by other wolves. The dead wolf was retrieved, a necropsy performed, and organ tissues examined by ADF&G wildlife biologists and an ADF&G veterinarian. Wounds were consistent with injuries sustained from intraspecific strife.



Figure 6. Photograph of a captured wolf, June 2015. Gretchen Roffler and wolf 201501 are featured in the photograph.

Table 1. Wolf captures on Prince of Wales Island, Alaska, June 2012–June 2015, by sex and age (J = juvenile, Y = yearling, A = adult).

Year	Season	Captures	Males	Females
2012	Spring	4	1A	2A, 1J ^a
2012	Fall	4	1A	2J, 1Y
2013	Spring	0	0	0
2013	Fall	1	1J	0
2014	Spring	2	1Y	1Y
2014	Fall	1	0	1Y
2015	Spring	2	1A	1A ^b
Totals		14	5	9

^a Wolf too small to instrument with a radiocollar.

^b Capture mortality.

Table 2. Trapping effort for the live-trapping and noninvasive methods, Prince of Wales Island, Alaska, June 2012–June 2015.

	Total days	Trap nights	No. sets/nodes	Wolves captured ^a	Wolves/100 trap nights
Live trapping					
2012 Spring	46	394	26	3	0.76
2102 Fall	22	1,987	68	4	0.20
2013 Spring	28	~1,500 ^b	60	0	0.00
2013 Fall	44	1,827	66	1	0.05
2014 Spring	28	413	36	2	0.48
2014 Fall	40	2,382	103	1	0.04
2015 Spring	30	1,445	71	1	0.07
Hair boards					
2012	69	1,216	38	16	1.32
2013	68	1,759	37	33	1.88
2014	66	4,420	72	37	0.84
2014 ^c (2013 nodes)	66	2,099	34 ^d	21	1.00

^a Wolves captured for live trapping = wolves captured and radiocollared, and for hair boards = the total number of wolf detections (includes recaptures).

^b Incomplete records. The number of trap nights is estimated.

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

^d Three nodes from 2013 could not be reestablished in 2014 due to road closures and construction.

Table 3. Average annual project costs for the live-trapping and noninvasive methods, time requirements, and average cost per captured or identified wolf, Prince of Wales Island, Alaska, 2012–2014.

Category	Live trapping	Noninvasive
Equipment	\$37,000	\$2,500
Operations	\$17,066	\$16,833
DNA analyses		\$10,000
Telemetry flights	\$24,000	
Personnel ^a	\$27,500	\$9,667
Average annual cost	\$105,566	\$39,000
Total 2012–2014	\$316,700	\$117,000
Days/year	90	80
Wolves captured/year ^b	3.7	16.7
Cost/wolf ^c	\$28,791	\$2,438

^a Salaries of full time permanent and temporary staff during the time period of trapping/hair sampling.

^b The average number of wolves captured and radiocollared per year for live-trapping, and the average number of unique individual wolves identified per year with DNA for noninvasive sampling.

^c Average cost = (annual cost x 3)/number of wolves captured and radiocollared ($n = 11$) or the number of wolves in the study area uniquely identified genetically from hair ($n = 48$).

Table 4. Fates, status, and number of days collared wolves ($n = 12$) were tracked on Prince of Wales Island, Alaska (6 June 2012–30 June 2015).

Wolf ID	Status	Fate	Days tracked
AF430	Mortality	Unreported human-caused	293
AF270	Mortality	Reported harvest	262
AM310	Mortality	Unreported human-caused	564 ^a
AM260	Mortality	Unreported human-caused	352
AF255	Mortality	Reported harvest	486
JF465	Mortality	Reported harvest	856
JF495	Mortality	Reported harvest	152
JM435	Unknown	Collar blow-off	314
YM330	Mortality	Intraspecific strife	237
YF250	Mortality	Reported harvest	168
201401	Alive	-	235
201501	Alive	-	22

^a Mortality date approximate.

REPRODUCTION

We checked a portion of den sites with documented use (between 1993 and 2004) during spring 2012–2014 (2012: $n = 3$, 2013: $n = 14$, 2014: $n = 12$), and all den sites in 2015 ($n = 24$). Between 1 and 3 active den sites were documented within the study area, in addition to 1 den site documented in 2014 on Tuxekan Island, outside of the study area (Appendix D). We documented reproduction by the Staney pack during spring 2013 when wolf AF255 produced a litter of 6 pups (Fig. 7). Five pups were observed in trail camera photos at the den site during May 2013, and 3 months later 6 pups were observed in photos from a trail camera in a different location within the pack home range. The Honker pack possibly had 2 breeding females in 2014 based on trail camera photos at den sites and direct observations. During late May–mid July, 2 Honker radiocollared wolves (JM435 and YM330), up to 2 unidentified wolves, and 3 pups were observed at a den site. At a different den site 8 km away within the Honker pack home range, 1 unidentified adult and 7 pups were observed on the ground the first week of June. During the subsequent October, the best count of the Honker pack included 16 wolves, so it is possible that these 2 groups of wolves united in the fall. However, by early November 2014 we no longer had radiocollared wolves representing the Honker pack (the radio collar of JM435 blew off, and YM330 dispersed), so we lack conclusive pack GPS locations and aerial observations after this date. During spring 2015, we documented 1 active den site within the Honker home range occupied by a minimum of 1 wolf pup.

HOME RANGES

Mean home range size of wolf packs using MCPs was 644 km^2 (range 470–944 km^2 , $SD = 261 \text{ km}$) and using KDE was 454 km^2 (range 292–644 km^2 , $SD = 178$; Table 5, Fig. 8). The radiocollared wolves that conformed to a home range represented 2 packs (Honker and Staney) that were largely consistent throughout our study period, as well as 1 additional pack (Ratz) that budded from the Honker wolves and occupied an adjacent territory for 10 months until the representative radiocollared wolf was killed. The Ratz pack consisted of 1 radiocollared wolf (AF430) and another unmarked wolf. In June of 2012, AF430 established a den on the northeast edge of the Honker home range approximately 18 km from the 2012 Honker active den. Locations for this wolf were concentrated around the eastern edge of the Honker territory with occasional forays back into the Honker home range until it was killed (unreported human-caused mortality) in late March 2013. Mean geographic centers of GPS locations for the Honker and Ratz packs were 15 km apart, and for the Honker and Staney packs 15.5 km apart.



Figure 7. Photograph of wolf pups at a den site on our study area from a trail camera, May 2013.

Table 5. Home range sizes of 3 resident wolf packs within the study area, Prince of Wales Island, Alaska (6 June 2012–30 June 2015) using minimum convex polygons (MCPs) and 95% adaptive kernel density estimators (KDEs).

Pack	No. radio collars	No. locations	95% KDE (km ²)	MCP (km ²)	Mean (km ²)
Honker	6	5,187	644	944	794
Ratz	1	1,038	426	470	448
Staney	2	2,069	292	518	505
Mean	3.0	2,765	454	644	549
SD	2.6	2,160	178	261	213

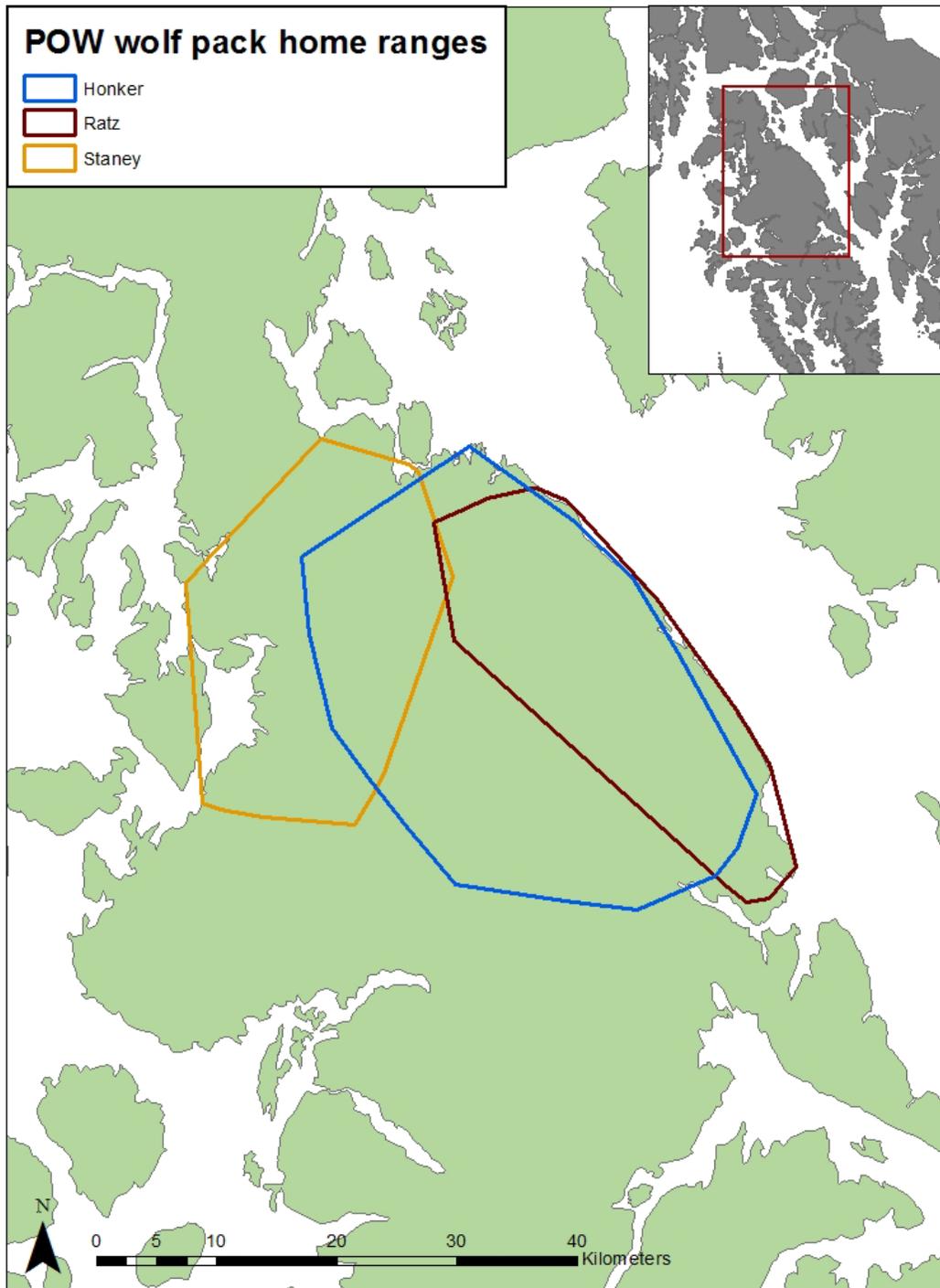


Figure 8. Wolf pack home ranges developed with minimum convex polygons (MCP), Prince of Wales Island, Alaska (6 June 2012–30 June 2015). The Honker and Staney pack home ranges were mostly stable throughout the study periods, whereas the Ratz pack budded from the Honker pack during spring 2012, and overlapped until being extirpated during spring, 2013.

Nonresident Wolves

Five of the 12 radiocollared wolves were classified as dispersers or extraterritorials at some point during the time they were monitored (Appendix B). Wolves' GPS locations during the time period they were in these categories were excluded from the calculations of the resident wolf home range territories. Wolf AM260 was captured within the Staney pack home range on 22 September 2012, and until 9 November 2012 it moved through and overlapped the Staney territory, thus, this lone wolf was classified as extraterritorial. During 9 November 2012–13 September 2013 the majority of its locations were focused on the southeast edge of the Staney pack, and appeared to describe a home range territory, thus the status of AM260 changed to resident.

Wolf 201401 (Memorial Beach pack) ranged from the north end of POW, where it was captured on 5 October 2014, to the south and east edge of our study area (as of May 2015; Fig. 9). This 2-year-old female wolf had been observed during June 2014–May 2015 with another wolf on trail camera photos, on the ground, and during aerial radiotracking, and for this time period was classified as a disperser. On 16 December 2014 wolf 201401 moved into the northeastern edge of our study area, ranging from Coffman Cove to the Kasaan Peninsula, and beginning in late March 2015 it appeared to establish a home range in the same area as the former Ratz pack. On 8 May 2015 the wolf accompanying 201401 (wolf 201501) was captured and radiocollared. Because 201501 was captured during the time the wolf location data reflects home range movements, it was classified as a resident, even though it had previously been a disperser (travelling with 201401, Appendix B).

Wolf YM330 dispersed from the home range of the Honker pack during fall 2014 and moved approximately 120 km to the south end of POW where it was killed by other wolves in late December 2014 (Fig. 9).

Wolf JF465 dispersed from the Honker home range in late May 2013 and was not relocated on subsequent telemetry flights. Using microsatellite DNA data, this wolf was identified in the harvest samples and had been legally trapped northwest of Hydaburg in February 2015. The GPS radio collar was recovered during an ensuing telemetry and ground-search effort, and locations downloaded from the radio collar revealed that JF465 had indeed dispersed from the Honker home range and established its own home range approximately 70 km to the south (Fig. 9).

Wolf AM310 dispersed from the Honker home range in February 2013 and was ultimately relocated in July 2015 in the Old Franks area, approximately 70 km to the south (Fig. 9). An attempt to salvage GPS locations from the recovered radio collar was largely unsuccessful due to collar damage. In summary, dispersal events occurred throughout the year as opposed to during one particular season, and ranged in length from 50 to 120 km straight-line distance, although the actual routes travelled reflect a much larger distance (e.g., approximately 240 km for YM 330).

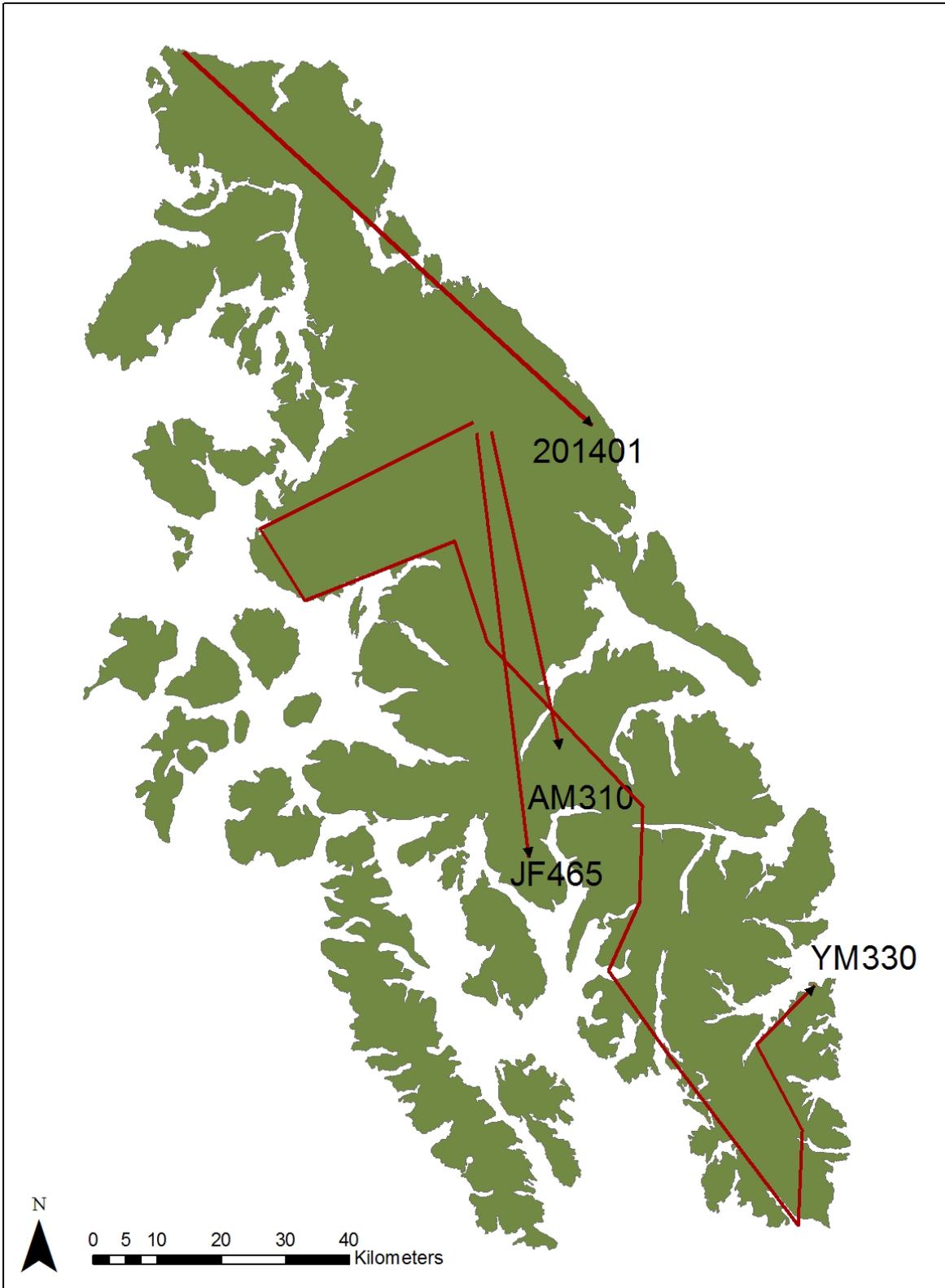


Figure 9. Generalized travel routes of 4 dispersing radiocollared wolves (201401, YM330, JF465, AM310), Prince of Wales Island, Alaska (6 June 2012–30 June 2015).

Dispersing wolves covered large portions of POW, but none traveled to adjacent islands within GMU 2 or crossed large bodies of water to reach areas outside of GMU 2.

MINIMUM COUNTS

Pack size of the 5 packs that occurred in the study area during the study ranged from 1 to 16 wolves, with an annual mean of 5.1 (SD = 1.7). Mean pack size in the fall (15 August–31 December) was 6.6 (range = 1–16, SD = 1.0), and in the spring (1 March–1 July) was 3.9 (range = 1–15, SD = 1.56 Table 6). The Honker, Ratz, Staney, and Memorial Beach packs were represented by radiocollared wolves (Table 5). The Sweetwater pack occurred on the northern boundary of our study area and was not represented by radiocollared wolves, thus our best evidence and minimum count for this pack came from the cameras deployed in the study area (Appendix C). The Memorial Beach pack did not move into our study area until spring 2015, and thus did not contribute to our study area fall minimum counts.

Fall minimum counts for the study area during 2012–2014 ranged between 19 and 23 (Table 6). In 2012, the minimum count was 19. The best count of the Honker pack ($n = 16$) occurred in early fall and included Honker radiocollared wolves AM310 and AF270, in addition to the Ratz wolf AF430. The Ratz pack wolf shortly thereafter separated and returned to her home range where it was observed aerially with an unidentified wolf in October 2012. In addition, during the same time, a wolf was struck and killed by a motorized vehicle nearby. Thus the minimum count was 13 for the Honker pack, and 3 for the Ratz pack. The best count for the Staney pack was based on trail camera photos documenting YF255 and 2 unidentified wolves.

Table 6. Fall minimum counts, seasonal counts, and mean pack size of wolf packs based on aerial and ground observations and cameras, Prince of Wales Island, Alaska (6 June 2012–30 June 2015).

Pack	2012		2013		2014		2015
	Spring	Fall	Spring	Fall	Spring	Fall	Spring
Honker	—	13	2	12	15	16	3
Memorial Beach	—	—	—	—	2 ^a	2 ^a	2
Ratz	1	3	1	—	—	—	—
Staney	—	3	7	8	1	1 ^b	2
Sweetwater	—	—	—	3	1	4	4
Mean pack size		6.3	3.3	7.7	4.8	5.8	2.8
Fall minimum count		19		23		21	

^a This pack was not located in the minimum count study area until spring 2015.

^b Radiocollared Staney wolf YF250 was harvested on 27 October 2014.

In 2013 the minimum count was 23 wolves. We observed 12 wolves in the Honker pack aerially during late fall, and 8 wolves in the Staney pack (including collared wolf YF255, an unidentified adult, and 6 pups) from trail camera photos during early fall. The Sweetwater pack had a minimum of 3 wolves based on trail camera photos.

The 2014 minimum count was 21 wolves. While the minimum count numbers were similar, the distribution of wolves shifted within the study area. The Staney pack was reduced to 1 known radiocollared wolf and was not observed with any other wolves during the radiotelemetry flights during fall until it was harvested on 26 October 2014. The Honker pack had 16 wolves, observed via telemetry flights during late October. We observed 4 wolves in the Sweetwater pack territory in trail camera photos taken during late fall (Appendix C).

POPULATION ESTIMATION FROM RADIOCOLLAR DATA

The fall minimum count (the maximum number of wolves observed in the study area) based on known wolf packs was 19 in 2012, 23 in 2013, and 21 in 2014 (Table 6). Expanding these minimum counts (empirical estimates) adjusted upwards by 29% to account for nonresident wolves in the area of POW and Kosciusko Islands (6,808 km²), we obtained fall population estimates for 2012: $\hat{N} = 108$, 2013: $\hat{N} = 131$, 2014: $\hat{N} = 120$ (Table 7). Because we used minimum counts, we had no measure of variation for the estimate. Thus, we could not calculate a coefficient of variation for these estimates.

Following procedures previously implemented by Person et al. (1996; wolf home range model), we estimated the fall wolf populations for the same area (POW and Kosciusko Islands; 6,808 km²) from the number of known packs, average pack size, and average home ranges (Table 7). We used these parameters in the wolf home range model for 2012–2014 (Table 7): 1) area of POW and Kosciusko Islands (6,808 km² = A); 2) year-specific values for average home range size (2012: $HR = 726$ km², 2013: $HR = 478$ km², 2014: $HR = 415$ km²); 3) year-specific values for the proportion of home range overlap (2012: $\alpha = 0.19$, 2013: $\alpha = 0.05$, 2014: $\alpha = 0.06$), and 4) year-specific values for the average number of wolves per pack (W_{pack}). The proportion of nonresident wolves (β) was 0.29 for the 2012–2014 estimates. Thus, the number of wolves estimated using the wolf home range model were as follows (Table 7): 1) 2012: $\hat{N} = 103$, SE = 64, (95% CI = 0.0–229 wolves/1,000 km²; CV = 0.63; 2) 2013: $\hat{N} = 163$, SE = 60, (95% CI = 45–281 wolves/1,000 km²; CV = 0.37; and 3) 2014: $\hat{N} = 143$, SE = 103; (95% CI = 0.0–345 wolves/1,000 km²; CV = 0.75).

To obtain fall population estimates for POW and Kosciusko Islands, we averaged the empirical and home range model estimates (2012: $\hat{N} = 106$, 2013: $\hat{N} = 147$, 2014: $\hat{N} = 131$). Because the empirical estimates had no variation, we could not calculate a coefficient of variation for these estimates.

Table 7. Results of year-specific empirical and home range models and parameter values used for estimating the wolf population for fall, 2012–2014.

Estimation method		Year					
		2012	SE	2013	SE	2014	SE
Wolf home range model							
<i>A</i>	Area (km ²)	6,808	0	6,808	0	6,808	0
<i>HR</i>	Ave home range size (km ²)	726	25.8	478	26.5	415	70.7
α	Prop. HR overlap	0.19	0	0.05	0	0.06	0
W_{pack}	Ave no. wolves in pack	6.3	3.8	7.7	2.6	5.8	4.0
β	Prop. dispersers (0.29)	0.29	0.09	0.29	0.09	0.29	0.09
\hat{N}	Wolf estimate	103	64	163	60	143	103
CI	95% CI for \hat{N}	(0, 229)		(45, 281)		(0, 345)	
Empirical estimate							
	Minimum count in study area	19		23		21	
	Empirical estimate (\hat{N}) for study area (1,683 km ²) ^a	26.8		32.4		29.6	
	Wolf density (<i>D</i>) in study area (per 1,000 km ²)	15.9		19.2		17.6	
\hat{N}	Wolf estimate (6,808 km ²)	108		131		120	
\hat{N}	Average (empirical and home range)	106		147		131	

^a Minimum count plus 29% for nonresident wolves.

NONINVASIVE DNA-BASED POPULATION ESTIMATION

Sample Collections

We collected hair samples at 23 (62%) of 37 nodes in 2012, 27 (75%) of the 36 nodes in 2013, and 41 (57%) of the 72 nodes in 2014. Of these hair samples, wolf hair was collected at 16 (43%) of the nodes in 2012, 15 (42%) of the nodes in 2013, and 19 (26%) of the nodes in 2014. The number of unique wolves identified genetically was higher in 2013 ($n = 21$) and 2014 ($n = 20$) than in 2012 ($n = 11$). Increasing the hair board sampling area and node density in 2014 resulted in more wolf hair samples ($n = 108$) than in 2012 ($n = 74$) or 2013 ($n = 86$), and increased the number of wolves redetected (2012: $n = 6$, 2013: $n = 8$, 2014: $n = 10$).

To assess the contribution of increased sampling area and intensity on trapping success, we compared 2014 sampling results using all 72 nodes to results using data from only the nodes previously used in 2013 ($n = 34$; 3 nodes could not be reestablished due to road closures or construction). The trapping success (number of wolf detections via DNA identification/100 trap nights) declined in 2014 compared to 2013 (Table 2) when comparing the total number of nodes used each year. Using sampling information from the 34-node data set in 2014, trapping success was higher (1.00 wolf detections/100 trap nights) than the 2014 full 72-node data set (0.84 wolf detections/100 trap nights), but still lower than the 2012 and 2013 node data sets (1.32 and 1.88 wolf detections/100 trap nights, respectively; Table 2). Directly comparing hair board sampling results from 2013 and 2014 (using the 2013 nodes) demonstrated a decline in the number of wolf detections (33 in 2013, 21 in 2014; Table 2). Five of the 18 new nodes established in 2014 within the 2012–2013 study area resulted in wolf detections (28%), whereas only 2 of the 19 nodes in the expanded study area detected wolves (11%).

Sampling in 2012 resulted in an insufficient number of recaptures (only 5 wolves were redetected after initial detection) to produce a reliable population density estimate. The 8 recaptured wolves in 2013 consisted of 4 individuals detected twice, and 4 individuals detected 3 times. The 9 recaptured wolves in 2014 included 4 individuals detected twice, 3 individuals detected 3 times, and 2 individuals detected 6 times. The distance between sequential recaptures 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).

The average project cost per wolf in the study area uniquely identified from hair ($n = 48$) during 2012–2014 was \$2,438 (Table 3).

Genotyping

Species identification was performed on mtDNA sequences from the 64 hair samples collected in 2012, and 80 of the hair samples collected in 2013 (we performed the single-hair extraction protocol for the remaining 13 hair samples; see below). Genotyping success for species identification was 83.4% in 2012 and 91.3% in 2013. Forty-five of the 54 samples from 2012 were identified as canids, 8 as black bears (*Ursus americanus*), and 1 sample was mixed canid and bear. Of the 73 standard protocol extraction samples from 2013, 54 were identified as canids, 18 as black bears, and 1 as marten (*Martes americanus*).

Results from the PCoA analysis distinguished our samples identified as canids between putative wolves and dogs. Using microsatellites from the harvested wolves, the putative wolves identified from hair samples, and the 11 suspected dogs (5 in 2012 and 6 in 2013), we demonstrated that the dogs clustered together and apart from the known wolf samples (as well as the wolves identified from hair samples; Appendix E). Samples from the putative dogs had alleles across 5 of the microsatellite loci that we did not observe in our known wolf samples (wolves captured for

this study and harvested wolves). This analysis, along with our evidence from the photos at the nodes where these hair samples were collected, suggests these 11 individuals were dogs and not wolves. Thus, we dropped the putative dogs from the rest of the analyses.

We used the microsatellite panel to genotype the 40 hair samples identified as wolf from 2012, the 39 standard hair extraction samples from 2013, the 52 single-hair extraction protocol samples from 2013, and the 137 unscreened samples from 2014. The genotyping success rate (the percentage of samples that successfully amplified and passed quality control steps) was 66% in 2012, and produced 28 genotyped wolf samples representing 11 individuals (9 males and 2 females). The genotyping success rate in 2013 for the standard extraction samples was 83% and 21 individuals were identified (10 males and 11 females). The single-hair extraction samples had a considerably lower genotyping success rate at 23%, although 7 individuals were identified (4 were represented in the standard hair extraction samples, and 3 were previously undetected wolves). In 2014 we obtained genotypes from 44% of the samples representing 18 individuals (14 males and 7 females).

During the time period of the hair board sampling (fall 2012–2014), 48 wolves were identified from noninvasively collected hair samples. We also genotyped 93 tissue samples from wolves harvested in GMU 2 during the 2012–2013 and 2013–2014 annual hunting and trapping seasons. Fifteen of the wolves identified from hair samples were later redetected in the harvest samples. We also redetected 3 of the radiocollared wolves (JF495, AF270, and YF255) in the 2012–2013 harvest samples and 2 radiocollared wolves were redetected during hair sampling (YM330 and JM435 in 2014). Two wolves were detected across sampling years from hair samples (1 between 2012 and 2013, and 1 between 2013 and 2014).

Population Density Estimates

The density estimate from the fall 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 8). This model included 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 sex-specific coefficients indicated that the baseline detection probability for females was an order of magnitude higher ($\hat{g}_{0,F} = 3.42 \times 10^{-2} \pm 1.51 \times 10^{-2}$) than it was for males ($\hat{g}_{0,M} = 3.92 \times 10^{-3} \pm 1.93 \times 10^{-3}$) and that males tended to have a larger home range size or exhibited larger movements than females ($\hat{\sigma}_F = 2.33 \times 10^3 \pm 3.87 \times 10^2$, $\hat{\sigma}_M = 8.09 \times 10^3 \pm 2.10 \times 10^3$). 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). The estimated proportion of females in the

Table 8. Wolf population density and size estimates based on spatially-explicit, capture-recapture (SECR) hybrid mixture models within a study area defined by a 10-km buffer in 2013, and a 20-km buffer in 2014 around all node locations, Prince of Wales Island, Alaska. Model AIC values, delta, and weights are shown. Density values are presented \pm SE (95% CI).

Model	Model parameter specifications ^a	AIC _c	Δ AIC _c	AIC _{cwt}	Density (per 1,000 km ²)	CV _D	Study area expected \hat{N}
2013							
18	g0-k + sex, $\sigma \sim$ sex	544.97	0	1.000	24.5 \pm 6.8 (14.4, 41.9)	0.278	41.3 \pm 11.7 (24.0, 71.2)
4	g0-sex, $\sigma \sim$ sex	554.42	9.45	0.000	20.1 \pm 4.9 (12.6, 32.1)	0.242	33.8 \pm 8.3 (21.0, 54.4)
17	g0-k, $\sigma \sim$ sex	556.38	11.41	0.000	30.0 \pm 10.0 (15.9, 56.7)	0.333	50.5 \pm 17.3 (26.3, 97.1)
7	g0-bk + sex, $\sigma \sim$ sex	556.86	11.89	0.000	20.5 \pm 5.0 (12.7, 32.9)	0.246	34.5 \pm 8.6 (21.3, 55.8)
10	g0-b + sex, $\sigma \sim$ sex	557.57	12.60	0.000	22.8 \pm 6.4 (13.3, 39.2)	0.282	38.4 \pm 11.0 (22.1, 66.7)
13	g0-B + sex, $\sigma \sim$ sex	558.81	13.85	0.000	19.7 \pm 4.8 (12.3, 31.6)	0.243	33.2 \pm 8.2 (20.6, 53.6)
21	g0-K + sex, $\sigma \sim$ sex	558.99	14.02	0.000	20.2 \pm 4.9 (12.6, 32.2)	0.243	33.9 \pm 8.4 (21.1, 54.7)
16	g0-K, $\sigma \sim$ 1	559.14	14.17	0.000	23.3 \pm 6.3 (13.8, 39.3)	0.272	39.2 \pm 10.9 (23.0, 66.8)
6	g0-bk, $\sigma \sim$ sex	569.50	24.53	0.000	22.7 \pm 6.4 (13.3, 39.0)	0.280	38.3 \pm 10.9 (22.1, 66.3)
5	g0-bk, $\sigma \sim$ 1	571.16	26.19	0.000	19.0 \pm 4.5 (12.0, 30.2)	0.239	32.0 \pm 7.8 (20.0, 51.1)
2	g0-1, $\sigma \sim$ sex	571.75	26.79	0.000	21.6 \pm 5.8 (12.9, 36.1)	0.267	36.3 \pm 9.9 (21.5, 61.3)
2014							
16	g0-k, $\sigma \sim$ 1	414.30	0	0.378	9.9 \pm 3.0 (5.5, 17.7)	0.304	32.4 \pm 10.1 (17.9, 58.7)
5	g0-bk, $\sigma \sim$ 1	414.83	0.53	0.290	8.7 \pm 2.5 (5.1, 15.0)	0.281	28.6 \pm 8.2 (16.5, 49.6)
14	g0-Bk, $\sigma \sim$ 1	417.18	2.88	0.089	8.3 \pm 2.3 (4.9, 14.0)	0.272	27.3 \pm 7.6 (16, 46.5)
19	g0-K, $\sigma \sim$ 1	417.69	3.38	0.070	8.6 \pm 2.4 (5.1, 14.6)	0.275	28.2 \pm 7.9 (16.5, 48.4)
17	g0-k, $\sigma \sim$ sex	417.83	3.53	0.065	10.1 \pm 3.2 (5.6, 18.4)	0.312	33.3 \pm 10.6 (18.1, 61.3)
6	g0-bk, $\sigma \sim$ sex	418.53	4.23	0.046	9.0 \pm 2.6 (5.2, 15.7)	0.289	29.6 \pm 8.8 (16.8, 52.2)
15	g0-Bk, $\sigma \sim$ sex	420.57	6.27	0.017	8.6 \pm 2.4 (5.0, 14.7)	0.278	28.1 \pm 8.0 (16.3, 48.6)
20	g0-K, $\sigma \sim$ sex	420.93	6.63	0.014	8.8 \pm 2.5 (5.1, 15.2)	0.282	29.0 \pm 8.4 (16.7, 50.4)
1	g0-1, $\sigma \sim$ 1	422.24	7.94	0.007	8.0 \pm 2.1 (4.8, 13.3)	0.304	26.1 \pm 7.0 (15.6, 43.9)
11	g0-B, $\sigma \sim$ 1	422.29	7.99	0.007	9.0 \pm 2.6 (5.2, 15.6)	0.282	29.5 \pm 8.6 (16.9, 51.7)

^a An explanation of the symbols used for g_0 and σ : b = learned response, global response, step change after first detection; B = transient response; global response, depends on detection at preceding occasion (Markovian response); bk = animal x site response, site-specific step change; Bk = animal x site response, site-specific transient response; k = site learned response, site effectiveness changes once any animal caught; K = site transient response, site effectiveness depends on preceding occasion; sex = sex of the animal, cluster = assignment to Bayesian-generated genetic based on proportional probability of membership.

population was $57.4 \pm 12.7\%$. The second- and third-ranked models also included various combinations of these two coefficients, but did not have sufficient weight to warrant model averaging ($\Delta\text{AICc} = 9.45$ and 11.41 , respectively). Using the density estimate from the top-ranked model, the estimated fall 2013 population size of the study area ($1,683 \text{ km}^2$) was 41.3 ± 11.7 wolves (95% CI = $24.0\text{--}71.2$), and the predicted population size for GMU 2 (constituting POW, and all islands larger than $5 \text{ km}^2 = 9,025 \text{ km}^2$; Fig. 1) was 221.1 ± 61.4 wolves (95% CI = $130.0\text{--}378.1$).

The density estimate for fall 2014, based on the top-ranked model, was 9.9 ± 3.0 wolves/ $1,000 \text{ km}^2$ (95% CI = $5.5\text{--}17.7$ wolves/ $1,000 \text{ km}^2$; CV = 0.304 ; Table 8). This estimate was significantly lower than the previous year. In contrast to 2013, where the top model accounted for 100% of the AICc weight, there were several competing models for 2014. The top-ranked model for 2014, which had an AICc 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. However, the top-ranked model did not contain a sex-specific coefficient for either \hat{g}_0 or $\hat{\sigma}$, which were estimated at $2.03 \times 10^{-3} \pm 8.50 \times 10^{-4}$ and $7.89 \times 10^3 \pm 1.14 \times 10^3$, respectively. The sex-independent estimates for g_0 and σ for 2014 were not significantly different from those of the corresponding male-specific parameter estimates in 2013. The estimated proportion of females in the population was $25.0 \pm 10.8\%$, which was a substantial decrease from the previous year. Models ranked 2–5 also contained either a site-effectiveness coefficient (k), or a coefficient indicating a site-specific behavioral change (bk or Bk), on \hat{g}_0 . Sex does not appear as an important coefficient until model 5, which had an AICc weight of 0.06 . The model-averaged density estimate using the top 5 models ($\Sigma\text{AICc}_{\text{wt}} = 0.89$) was 9.24 ± 2.84 wolves/ $1,000 \text{ km}^2$ (95% CI = $5.13\text{--}16.64$ wolves/ $1,000 \text{ km}^2$). The model-averaged density estimate using all models with an $\text{AICc}_{\text{wt}} > 0$ (top 14 models) was 9.22 ± 2.87 wolves/ $1,000 \text{ km}^2$ (95% CI = $5.08\text{--}16.74$ wolves/ $1,000 \text{ km}^2$). Using the density estimate from only the top-ranked model, the predicted number of wolves in the 2014 extended study area ($3,280 \text{ km}^2$) was 32.4 ± 10.1 (95% CI = $17.9\text{--}58.7$) and 89.1 ± 27.1 (95% CI = $49.8\text{--}159.4$) for GMU 2.

To examine the effects of expanding the study area and sampling intensity in 2014, we fit models with the same parameter specifications using a truncated dataset 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 truncated 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 persists throughout the remainder of the study period. The density estimate using this model was larger (10.7 ± 4.1 wolves/ $1,000 \text{ km}^2$, 95% CI = $5.2\text{--}21.9/1,000 \text{ km}^2$) than the top-ranked full-data model (9.9 ± 3.0 wolves/ $1,000 \text{ km}^2$) but not significantly so. The density estimate using the 2013 nodes in 2014 produced a predicted population in a study area comparable to the one 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 9). Fitting the reduced data set to a model with identical parameterization as the top-ranked full-data model also resulted in a higher density estimate (11.1 ± 4.5 wolves/1,000 km²), but also was not significantly different. Increasing the size of the study area and the density of nodes also resulted in a density estimate with a substantially lower coefficient of variation for the estimated density parameter (0.304 vs. 0.365).

Discussion

Our objective was to compare 2 approaches (traditional and noninvasive DNA-based capture-recapture) to estimate wolf abundance in Southeast Alaska in terms of reliability, cost, and effort. The aerial radiotelemetry approach has been widely used by wolf researchers and managers since the 1970s and is still commonly employed in areas with open terrain (Fuller 1989, Ballard et al. 1997, Mech et al. 1998, Hayes and Harestad 2000, Adams et al. 2008), although generally expensive and time-consuming (Boitani 2003). DNA-based capture-recapture is an increasingly-used approach that has potential for application in more obscured terrain (Stenglein et al. 2010, Ausband et al. 2014, Stansbury et al. 2014). This research represents the first density estimate of wolves produced using data from hair traps (DNA based) and spatial capture-recapture methods. We found that in addition to having higher trapping success and lower costs than the traditional approach, the noninvasive DNA-based method produced a more statistically robust and precise population estimate of wolves.

POPULATION ESTIMATES USING THE NONINVASIVE DNA-BASED METHOD

Our criteria for evaluation of the population estimation methods are based on the potential application to long-term monitoring of wolves in Southeast Alaska. The noninvasive DNA-based method had many benefits over the traditional methods. We were able to obtain sufficient recaptures after 9 weeks of sampling to produce a population estimate along with a measure of precision by using SECR procedures, information essential for sustainable management of wolves. Population estimates using traditional methods (captures and radiocollaring wolves) were not possible to achieve during this short of time frame in our study environment. Another benefit of the noninvasive DNA-based method is detection of nonresident wolves. Traditional methods rely on observations of wolf packs represented by radiocollared individuals, thus nonresident wolves not associated with a pack have a low likelihood of being detected, particularly in a densely-forested environment. Nonresident wolves traveling through the study area, while cryptic to visual detection, may deposit hair on the hair traps. Therefore, density estimates produced with SECR theoretically represent all wolves in the study area, and not just the known pack members. The genetic data obtained from hair samples, in addition to identifying unique wolves, may also be used to construct pedigrees or to understand genetic structuring of

Table 9. Predicted 2014 wolf population estimates from the 10 most parsimonious models for Prince of Wales (POW) and Kosciusko Islands (6,808 km²), and Game Management Unit (GMU) 2 (9,025 km²). Values are presented ± SE (95% CI). The top models for each year were used for the fall wolf estimate.

	Model	Model specification ^a	POW + Kosciusko islands	GMU 2
2013	18	g0~k + sex, σ~sex	166.8 ± 46.3 (98.0, 285.3)	221.1 ± 61.4 (130.0, 378.1)
	4	g0~sex, σ~sex	136.8 ± 33.4 (85.8, 218.5)	181.4 ± 44.2 (113.7, 289.7)
	17	g0~k, σ~sex	204.2 ± 68.1 (108.2, 386.0)	270.8 ± 90.3 (143.5, 511.7)
	7	g0~bk + sex, σ~sex	139.6 ± 34.0 (86.5, 224.0)	185.0 ± 45.1 (114.6, 296.9)
	10	g0~b + sex, σ~sex	155.2 ± 43.6 (90.5, 266.9)	205.8 ± 57.8 (120.0, 353.8)
	13	g0~B + sex, σ~sex	134.1 ± 32.7 (83.7, 215.1)	177.8 ± 43.3 (111.0, 285.2)
	21	g0~K + sex, σ~sex	137.5 ± 33.4 (85.8, 219.2)	182.3 ± 44.2 (113.7, 290.6)
	16	g0~k, σ~1	158.6 ± 42.9 (94.0, 267.6)	210.3 ± 56.9 (124.5, 354.7)
	6	g0~bk, σ~sex	154.5 ± 43.6 (90.5, 265.5)	204.9 ± 57.8 (120.0, 352.0)
	5	g0~bk, σ~1	129.4 ± 30.6 (81.7, 205.6)	171.5 ± 40.6 (108.3, 272.6)
2014	16	g0~k, σ~1	67.2 ± 20.4 (37.5, 120.3)	89.1 ± 27.1 (49.8, 159.4)
	5	g0~bk, σ~1	59.4 ± 16.7 (34.6, 101.9)	78.7 ± 22.1 (45.8, 135.1)
	14	g0~Bk, σ~1	56.6 ± 15.4 (33.6, 95.5)	75.1 ± 20.4 (44.5, 126.7)
	19	g0~K, σ~1	58.6 ± 16.1 (34.5, 99.5)	77.6 ± 21.4 (45.7, 131.9)
	17	g0~k, σ~sex	69.0 ± 21.5 (38.0, 125.5)	91.5 ± 28.5 (50.4, 166.3)
	6	g0~bk, σ~sex	61.5 ± 17.8 (35.3, 107.1)	81.5 ± 23.6 (46.7, 142.0)
	15	g0~Bk, σ~sex	58.4 ± 16.3 (34.2, 99.7)	77.4 ± 21.5 (45.3, 132.2)
	20	g0~K, σ~sex	60.2 ± 17.0 (35, 103.6)	79.8 ± 22.5 (46.4, 137.3)
	1	g0~1, σ~1	54.2 ± 14.4 (32.6, 90.4)	71.9 ± 19.1 (43.2, 119.8)
	11	g0~B, σ~1	61.3 ± 17.5 (35.4, 106.1)	81.3 ± 23.2 (47.0, 140.6)

^a An explanation of the symbols used for g₀ and σ: b = learned response, global response, step change after first detection; B = transient response; global response, depends on detection at preceding occasion (Markovian response); bk = animal x site response, site-specific step change; Bk = animal x site response, site-specific transient response; k = site learned response, site effectiveness changes once any animal caught; K = site transient response, site effectiveness depends on preceding occasion; sex = sex of the animal, cluster = assignment to Bayesian-generated genetic based on proportional probability of membership.

the population, levels of genetic diversity, and gene flow among regions. We were able to determine sex composition of sampled wolves from the genetic data, a characteristic not always possible to identify from visual observations. Importantly, data collection for the SECR population density estimate was more efficient and economical and, therefore, would be more feasible to use in population monitoring efforts requiring repeated estimates. Moreover, the noninvasive DNA-based method was less sensitive to violations of assumptions (discussed below) than the traditional methods, and thus more robust.

There are a number of assumptions associated with the SECR methods. Like traditional capture-recapture (CR) models, SECR assumes both geographic and demographic closure; however, SECR is much more flexible with the assumption of geographic closure. Traditional CR models assume that there is no movement of animals into or out of the study area (no immigration or emigration) and that all animals are available for sampling during the course of the study (Otis et al., 1978). SECR relaxes this by assuming no permanent immigration or emigration during the study period. This allows for the possibility of animals having home ranges that are not fully encompassed by the study area boundaries and therefore those animals may not be available for sampling during one or more occasions due to temporary movement outside the study area. GPS collar data indicates that although the home ranges of the resident radiocollared wolves were completely encompassed by the study area, a few wolves dispersed out of, or into the study area during the hair sampling period. In 2014 YM330 permanently dispersed out of the study area in late November after leaving hair samples at a hair board node. Animals that were identified during the study period but permanently dispersed out of the study area during the sampling period would lead to a violation in this assumption if the removal was not accounted for, causing a negative bias in the baseline detection probability and, consequently, a positive bias in the density and population size estimates. In another case, wolf 201401 moved into the study area in mid-December 2014, but did not visit any sampling nodes.

Like traditional CR models, SECR also assumes complete demographic closure during the course of the study period. As our study period takes place during the annual hunting and trapping seasons, 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 sampling period; however, 2 known animals were removed during the 2013 study period. These removals would possibly result in a positively biased population density estimate for that year.

The SECR method assumes that the distributions of animal activity centers and animal movement are independent. As wolves are pack animals, it is certain that this assumption was violated during our study. Although mean parameter estimates are not likely to be affected, violating this assumption results in overdispersion and, thus, variance estimates would be biased

low (Efford 2004) with 95% confidence intervals that are narrower than they should be. However, this would not affect our result of the 2014 density estimate being significantly lower than that of 2013 based on the bootstrapped 95% confidence intervals of the difference between estimates. Methods exist to estimate and compensate for the level of non-independence in the data, such as the median- \hat{c} statistic in Program MARK (White and Burnham, 1999) and model selection based on quasi-AIC (QAIC), though these methods have not been implemented for SECR models in the R secr package (as of version 2.9.5).

An assumption that is commonly listed for SECR models is that animals occupy home ranges that are approximately circular in shape. This assumption is based on the use of a detection function that relates the probability of detecting an animal based on the distance between the detector and the animal's activity center or home range center and the implicit assumption that this relationship is the same in all directions. Although one study (Ivan et al. 2013) suggests that SECR estimates of density are more likely to be biased low (error was within $\pm 20\%$ in 43–53% of simulations) as the home range shape becomes highly irregular or substantially elongated (e.g., a 1:4 ellipse), SECR methods are generally very robust to violations of this assumption and can accommodate home ranges that are not circular, provided that traps are placed randomly with respect to the location of activity or home range centers. Violations of this assumption are more likely to result in larger variance estimates (i.e., parameter estimates with lower precision), than to result in significant bias (Efford 2004). Although the estimated home range shapes of telemetered animals in the current study were somewhat oval or elliptical in shape, the shapes were not substantially elongated (average ratio of the x and y axes was 0.96). Therefore, we do not suspect our estimates to be significantly biased due to the shapes of the home ranges of wolves in our study area.

One concern with the SECR approach is whether the same sample size requirements for the robust estimation of an animal's home range should be applied to SECR models as well. The sigma parameter is a spatial-scale parameter that describes the rate of decrease in detection probability with the distance between the detector and an animal's activity center, and can be used to estimate the area that would be expected to include a certain proportion of points from a circular bivariate distribution corresponding to a specific detection function. Although this proportionality is often used to describe the home range of the subject animals, the area used by the subject animals over the course of the study may not necessarily represent true home range. For wide ranging animals or for relatively short study periods, the area of activity used by the animal during the study period will likely represent only a portion of the true home range, and thus, the area estimated using sigma would be proportionally smaller.

The misconception that sample size requirements for home range estimation must also be applied to SECR methods has led to the rejection of the SECR technique in some studies (e.g. Morton et al. 2015) due to a perceived lack of data to robustly estimate the sigma parameter. In applying SECR models to our data, we do not use sigma to estimate an actual home range size, but rather

the spatial scale of detectability during the study period. To this end, a sample size of at least 20 recaptures is recommended for robust parameter estimation (Efford et al. 2004; Efford et al. 2009). Borchers and Efford (2008) show that even at these low captures rates, MLE estimates of sigma have negligible bias (0.75%), though precision is substantially higher as capture rate increases. In both 2013 and 2014, we met or exceeded this recommended value with 26 and 20 recaptures, respectively. Additionally, wolves belonging to the same pack are likely to have the same relative spatial detection parameters, and thus, a robust estimate for a single animal would serve well for the remaining animals in the same pack.

Furthermore, the estimation of activity area size using sigma assumes that the center of activity remains fixed. When transience or dispersal exists, the sigma parameter cannot be used to directly estimate activity area or home range size as they would be substantially positively biased by the additional variance associated with the non-stationary activity centers. However, Royle et al. (2015) has shown that density and population size estimated using SECR methods are extremely robust to even “pathological levels of movement,” with relative biases of <1%.

Other assumptions made by SECR models are that animals do not lose their marks and are correctly identified (which is the same for traditional CR methods), trap locations are recorded accurately, each animal has an activity or home range center, detectors are randomly placed with respect to these activity centers, and that there is no unmodelled heterogeneity. We do not have any evidence to suggest that any of these remaining assumptions have been substantially violated.

The increase of our sampling area in 2014 is a consideration when interpreting density estimate results. The fall 2014 wolf density estimate was significantly lower than for 2013; however, using the 2014 truncated data (representing only the 2013 nodes) provides a more direct comparison to the 2013 density estimate. The 2014 truncated data produced a higher density estimate (10.7 ± 3.9 wolves/1,000 km², 95% CI = 5.3–21.4 wolves/1,000 km²) than when using the full data set, and the predicted GMU 2 population estimate was correspondingly higher (96.5 ± 35.2 , 95% CI = 48.3–193.0). These results still suggest a substantial difference among sampling years, although less severe than when comparing to the full 2014 sampling area. It is possible that the density estimate for the 2013 hair sampling area, which was considerably smaller than the 2014 sampling area, was biased high, translating to an overestimate of the GMU 2 population in 2013. We doubled the sampling area in 2014 to 36% of the GMU, which we would expect to be more representative of the unit as a whole, offering a more accurate assessment of wolf densities on POW.

ADF&G and the USFS manage wolves at the GMU for seasons and bag limits, so it is desirable to monitor population trends at the GMU level. Given this reality, we were interested in estimating the number of wolves in GMU 2, but to sample the entirety of the unit was logistically prohibitive. Therefore, we chose to sample a smaller portion of the unit that we believed was

representative of the average conditions of the unit as a whole. Thus, we predicted wolf population size for GMU 2 (constituting POW, and all islands larger than $5 \text{ km}^2 = 9,025 \text{ km}^2$; Fig. 1) based on densities measured on the study area. For this prediction to be valid, one has to assume the average densities on our study area are similar for the predicted area. We have no evidence to question this assumption.

POPULATION ESTIMATES USING THE TRADITIONAL APPROACH

The traditional capture-and-radiocollar approach has been used on POW during different time periods throughout the past 3 decades (Person et al. 1996, Person 2001, Person and Russell 2008, Person and Russell 2009), and data acquired using this method was the basis for the 1994 wolf population estimate in GMU 2. This approach can produce a population estimate given adequate sample sizes of radiocollared wolves which are necessary to generate the required pack home range sizes, mean number of wolves per pack, and estimate the proportion of nonresident wolves in the population in addition to associated variance estimates. Another benefit to the traditional method of radiocollaring wolves is acquisition of GPS location data which is useful for spatial analyses including movement patterns and habitat use. Finally, if enough wolves in the population are represented, vital rates such as annual survival may be estimated. This method is widely used in Alaska (Gasaway et al. 1983, Ballard et al. 1987, Bortje and Stephenson 1992, Ballard et al. 1997, Mech et al. 1998, Adams et al. 2008), and to monitor the recovery of wolves in the northern Rockies (Mitchell et al. 2008, Murray et al. 2010, Gude et al. 2012).

The drawbacks to this approach include underrepresentation of nonresident wolves in the radiocollared population, poor visibility for aerial observations, and difficulties in obtaining a sufficient sample size of radiocollared wolves in our study area, as capturing and radiocollaring wolves in Southeast Alaska is labor intensive and expensive compared to areas where helicopter-based capture is more feasible. Radiocollared wolves are generally associated with packs, and, therefore, population estimates based on observations of marked individuals may exclude nonresident wolves. Indeed, 10 of the 12 radiocollared wolves in this study were associated with established packs at the time of capture, and one of the 2 captured nonresidents was associated with a pack member, although had not yet established a home range.

The above-mentioned drawbacks affect both the minimum count and wolf home range model methods. A shortcoming specific to the empirical method is that it relies on minimum counts, which only reflect the minimum number of animals known to be alive during the sampling time frame, and population estimates based on this value are therefore likely to be biased low. An assumption of this method is that the bias may be accounted for by adjusting the minimum count upwards by the proportion of nonresident wolves in the population. However, this value potentially varies from year to year, and because the population estimate is sensitive to this value, using a static or assumed value of 0.29 potentially may create a source of inaccuracy in the population estimates. Furthermore, it is feasible that resident wolves have a higher

probability of being captured because they are more likely to travel on roads and display marking behavior (Vila et al. 1994, Barja et al. 2004). Thus, it is necessary to acknowledge that a possible bias in capture probabilities among classes of wolves may reduce the accuracy of wolf population estimates (Burch et al. 2005, Wydeven et al. 2009).

The wolf home range model has disadvantages as well, one of which is that the results likely lack the precision to detect changes in the population among years. The coefficient of variation ranged from 0.369 to 0.749 for 2012–2014 compared with 0.278 in 2013 and 0.304 in 2014 for the DNA-based SECR approach. The coarseness of the results is partially attributed to the low sample size of radiocollared wolves, which renders estimating the proportion of nonresidents in a population, annual home range size, and the proportion of home range overlap imprecise. The number of resident radiocollared wolves in the study area during 2012–2014 ranged from 3 to 5, but by November 2014, radiocollared wolves had either died or dispersed, and thus could not be used for calculating home range size. The proportion of home range overlap ranged from 0.5 to 0.19 during 2012–2014, which reflects the dynamic nature of wolf pack boundaries, but fluctuations in values influence the population estimates from the wolf home range model. As results from this method were only previously published for the fall of 1994 (Person et al. 1996), we do not have variation in values among sequential years for either the population estimate or model inputs for comparison.

A disadvantage of the wolf home range method is it is sensitive to violations of model assumptions. One assumption of the model is that all available space is occupied by wolf packs; however we have evidence of vacant regions within our study area during the annual sampling period. The Staney pack in the western half of the study area had a minimum of 8 wolves at its highest count during the fall of 2013. Based on aerial and trail camera observations, the Staney home range was likely vacant beginning in late October 2014 (when YF255 was harvested) and was not reoccupied by a pack during our study period. This observation was corroborated by the noninvasive sampling results. Wolf hair samples were collected from multiple nodes in the Staney home range in 2013, but only one individual was detected on only one occasion from hair samples during fall 2014, possibly representing a nonresident wolf. There had been substantial wolf harvest in the study area since the 2013 fall population estimate. Fifty-seven wolves were harvested in GMU 2 legally by trapping and hunting in regulatory year 2013 (fall/winter of 2013–2014), 6 of which were from areas in the Staney home range in our study area. Assuming consistent occupancy of wolf pack home ranges throughout the study area can lead to an overestimate of the population, a drawback that was acknowledged by Person et al. (1996).

Due to the nature of conducting aerial surveys of densely forested areas such as Southeast Alaska, visibility of marked wolves and their associated pack members is often low. Indeed, only 10 of the 44 observations used to generate the 2012–2014 fall minimum counts were obtained from telemetry flights (Appendix C), and only 33% of the completed flights produced any visual observations of wolves. The telemetry flights were necessary to download the GPS data from

wolf radio collars, but did not produce reliable counts of pack numbers. The heavily timbered landscape in GMU 2 also contributes to the difficulties in obtaining sufficient sample sizes of wolves for radiocollaring. In this region it is not possible to use helicopters for capture and chemical immobilization, a commonly applied and efficient method to mark wolves for monitoring and research in other areas of North America.

COMPARISON OF COSTS AND EFFICIENCY OF POPULATION ESTIMATION APPROACHES

Comparing the 2 approaches in terms of costs demonstrated that the noninvasive DNA-based method is more economical (Table 3). Operational costs were fairly similar, but the equipment costs of trapping wolves were higher, particularly for the GPS collars. Radiotracking flights were also a considerable expense. The staffing expenditures were higher for live-trapping because daily trap checks require staff (2–3 people) to work 7 days a week. In contrast, the hair board monitoring required only 2 people working 3–4 days a week in 2012–2013, and 3 people in 2014 because of the expanded study area. Compared to the daily checks required for live-trapping, the weekly checks employed during the hair board monitoring translated to fewer staff hours, less driving, and consequently, less fuel spent. The hair boards are inexpensive to produce, but lure is still required and costs approximately \$3,000 per year. Overall, capturing and radiocollaring wolves was nearly 12 times more expensive than identifying individual wolves genetically.

Overall, the traditional approach required more effort and more of a time commitment than the noninvasive DNA-based approach. The live-trapping effort in spring 2012 had similar success rates (0.76 wolves/100 trap nights) as the hair board method in 2014 (0.84 wolves/100 trap nights). After spring 2012, we experienced generally declining rates of wolf captures despite increased effort over time. Comparing trapping seasons, spring was a more successful time for radiocollaring wolves than the fall. This result was counterintuitive, as the spring population size for wolves is at its lowest level for the year, whereas during fall, it is the highest. Wolf pack home ranges are also considerably smaller during spring, consisting of a core area of the more extensive fall home range. As a result, we would expect trapping success to be lower in the spring because of reductions in large scale movements across areas where traps are set, thus lowering the chances of capture. Trapping success might be lower in the fall because wolves on POW use spawning salmon (*Onchoryncus* spp.) as food (Darimont et al. 2008), and may be localizing on streams during that time (Person 2001), and not traveling on the road system where live-traps are deployed. GPS location data support this hypothesis, as some radiocollared wolves remain in one spot (usually on or near a stream) for extended periods during our trapping season.

Capture efforts conducted in the early 1990s and 2000s were more successful than during our current study period (Person 2001). On average, 829 trap nights were required to capture a wolf during 2012–2014, and the average rate of capture was 1 wolf per 20 days. In comparison, during a 10-month stretch from early 1993 to late 1994, 24 wolves were captured and radiocollared in GMU 2. This effort represented ~4,700 trap nights with a mean capture rate of 1

wolf per 11 days (an average of 196 trap nights were required to capture each wolf; Person 2001). The increased trapping effort needed to capture and radiocollar wolves during our study could reflect a variety of conditions, including a lower wolf population density in the study area, changes in wolf behavior such as becoming aware of land trap sets, or other unknown reasons.

The comparison between methods assumes that the only parameter of interest is an estimate of abundance. Naturally, radiocollaring wolves yields additional information (e.g., home range size, movement patterns) that assists with interpreting the results of the SECR. However, in the absence of radiocollar data, the SECR approach provides information on the spatial movement patterns (including the σ parameter proportionally related to home range size) of individuals in their capture histories, a further strength of this method.

CHANGES IN WOLF POPULATION ABUNDANCE

Based on multiple lines of evidence, we concluded there was a decline in wolf population abundance over the past 2 decades in northcentral POW. We compared past and current population estimates in the wolf population in a similar area. During fall 1994, Person et al. (1996) estimated wolf density in fall for POW and Kosciusko islands was 39.5 wolves/1,000 km², considerably higher than the density estimates we produced with the noninvasive DNA-based method during this study in 2013 ($\hat{N} = 24.5 \pm 6.8$ wolves/1,000 km²) and in 2014 ($\hat{N} = 9.9 \pm 3.0$ wolves/1,000 km²). Estimates from 1994 were also substantially higher than those produced during this current study when using the same methods (average 2012–2014 $\hat{N} = 18.7$ wolves/1,000 km²).

The apparent decline in the GMU 2 wolf population over the past 2 decades could be due to a variety of factors, such as increased wolf harvest (reported and unreported), reduced reproduction, changes in prey vulnerability, increased disease rates, or a combination of these. An example of a complex factor contributing to a long-term decline in the wolf population is high levels of unreported human-caused mortality in combination with reported harvest. During our study period, we documented 3 cases of unreported human-caused mortality out of 12 radiocollared wolves (25%). Five other radiocollared wolves died from reported legal harvest.

Another potential factor that could contribute to a decline in the wolf population is a decrease in prey abundance. Because wolf abundance is believed to be largely limited by the availability of vulnerable ungulate prey (Keith 1983, Fuller 1989, Fuller et al. 2003), a decline in Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) could affect wolf abundance. Because availability of vulnerable ungulate prey is difficult to measure, an ungulate biomass index may be used as a proxy (Fuller et al. 2003). We compared wolf population estimates from methods implemented in this study and wolf abundance predicted by ungulate biomass regression models (Appendix F). The 2013 fall wolf population estimate from SECR ($\hat{N} = 221.1 \pm 61.4$ wolves (95% CI = 130.0–378.1)) was comparable to the current (2015) ungulate biomass regression model prediction ($\hat{N} = 239$) suggesting that wolf populations are responding to availability of ungulate

biomass. However, the 2014 SECR wolf population estimate was substantially lower (89 ± 27.1 (95% CI = 49.8–159.4) wolves), suggesting some other factor is more influential to wolf abundance. If wolves in GMU 2 were limited mostly by ungulate abundance, 2014 populations would be expected to be comparable to the 2013 estimates.

In GMU 2, few studies based on actual deer observations have been conducted to estimate deer abundance; instead, habitat-based values and pellet counts are used as crude indices. We lack evidence that deer abundance decreased during this study period, although long-term broad-scale succession patterns predict a decline in the deer population resulting from stem exclusion (Person and Brinkman 2013). However, the wolf population could decline, even in the absence of a decline in deer abundance, if deer have become less vulnerable to wolf predation because winters are less severe. In the upper Midwest United States evidence indicates that deer are more vulnerable when they congregate (yard) during severe winters, and less susceptible to wolf predation during mild winters (Nelson and Mech 1986, Fuller 1991, Mech and Peterson 2003). In Southeast Alaska, Farmer et al. (2006) demonstrated that during the most severe winter (1998–1999) of their study (1997–2000) young deer (<1 year old) experienced nutritional stress on Heceta Island that coincided with the period of highest mortality from wolf predation. Winters during our study period were relatively mild, but we lack empirical data to test this hypothesis.

IMPROVING THE NONINVASIVE DNA-BASED METHOD AND FUTURE DIRECTIONS

We encountered some drawbacks to the noninvasive DNA-based method during the course of this research. The first year of the hair-board monitoring, we didn't get sufficient numbers of recaptures of individual wolves from hair samples, resulting in no population estimate for 2012. Some additional shortfalls with the method were identified in the first year of this study. For example, hair boards were checked less frequently (once every 10 days instead of every week), they were not visibly marked (and thus became difficult to relocate after a heavy snowfall), and boards were not anchored (which allowed wolves to move them), resulting in lost hair boards and potential hair samples that could not be recovered. Beginning in 2013, we checked hair boards at a higher frequency (once a week) in order to increase our chances of obtaining more hair samples and detecting recaptures. In 2013 we also implemented protocol requiring hair boards to be marked with flagging and wired to stationary objects and/or nailed into the ground. These changes resulted in collection of sufficient hair samples to estimate wolf population density in the study area with the SECR approach.

Another improvement implemented during the course of this study was increasing the intensity of the sampling effort in 2014. We increased both the size of the study area and the node density, resulting in a higher numbers of wolf samples collected ($n = 108$) than in 2012 ($n = 74$) or 2013 ($n = 86$), and an increased number of unique wolves redetected (2012: $n = 6$, 2013: $n = 8$, 2014: $n = 10$). However, trapping success (detections/trap/100 days) declined in 2014 (0.84 wolves/100

days) in comparison to 2012 (1.32 wolves/100 days) and 2013 (1.88 wolves/100 days). The lower trapping success experienced in 2014 could reflect a variety of conditions, including a reduction in the wolf population in the study area, a redistribution of wolves in the study area (the Staney Creek home range was not occupied by a wolf pack in 2014), changes in wolf behavior, or other unknown reasons. We obtained density estimates over a larger area, and the lower number of detections could also reflect the heterogeneity of wolf distribution throughout the sampling area, specifically that wolves occur in lower densities on some areas (e.g., where former pack home ranges are unoccupied, or habitat is less favorable) and higher densities in other areas. Therefore, the lower detection rate is not necessarily indicative of failure of the method, but instead a more accurate representation of wolf densities in northern POW.

Finally, we found that implementing screening protocols increased the genotyping success rate. The first of these protocols was to separate out the hair samples that were suspected to consist of more than one individual. This situation can occur when multiple wolves visit a node and sequentially roll on hair boards, as evidenced by photos from trail cameras stationed at hair board nodes. The genotyping success rate increased from 66% in 2012 to 83% in 2013 when multiple-wolf samples were analyzed separately (see methods and results). Secondly, we determined that the mtDNA species identification step resulted in higher genotyping success rates. This process was bypassed in 2014 in the interest of producing a timely population estimate for consideration by the USFWS ESA status review. As a result of attempting to genotype all DNA samples extracted from hair, success rate was reduced to 48.3%. In future monitoring efforts, it is recommended to retain the species identification step in the genotyping process.

An interesting revelation from this research was that information from trail cameras provided a relatively greater contribution to the fall minimum counts than aerial observations. Use of cameras has great potential in density, relative abundance, and occupancy studies, particularly of cryptic species (Long et al. 2011, Burton et al. 2015). In addition to repeating hair board monitoring during fall 2015 using the same array as in 2014, our future research plans involve distributing trail cameras throughout the study area to monitor changes in occupancy and continuing to monitor known den sites. We will also attempt to learn how wolves use the hair boards, and see if we can detect any biases in probability of detection among sex and age classes of wolves.

CONCLUSIONS

For estimating wolf population density in an area for either a short time period, or over multiple years as part of a monitoring effort, the noninvasive DNA-based method proved to be more robust, precise, efficient, and cost-effective than the traditional method. As this research represents the first attempt to estimate wolf population density using this method, further work is required on POW and in other areas for comparison and further method refinement. Available staffing and access to hair snare node locations are the main limitations to the size of a potential

study area. Because success of this method is dependent upon obtaining a sufficient number of recaptures, we recommend increasing the density of nodes throughout the study area, especially in regions where wolf density is believed to be lower than the average in our study area. It is generally recognized that obtaining accurate population estimates for wolves in areas of dense cover and little snow is one of the most challenging monitoring situations of any species (Boitani 2003). Continued efforts to evaluate the DNA-based capture-recapture methods will allow us to gain insight into how to best estimate population densities of a wide-ranging carnivore with dynamic population attributes. Specifically, application of this method would benefit from a better understanding of how density estimates are influenced by varying levels of occupancy within a study area, and the effects of habitat heterogeneity. With this research we hope to advance the development of methods and their application to enhance monitoring efforts of this cryptic creature.

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Appendices

Appendix A. Definition of predictor variables used in detection models (modified from Efford 2014, secr 2.9 overview).

Predictor	Description	Notes
b	Learned behavioral response	Global response. Animals become attracted to (trap happy) or repelled by (trap shy) detectors after the first detection (step change) throughout the entire study area. Response persists throughout duration of study.
B	Transient behavioral response	Global response. Response depends on detection at each preceding occasion (Markovian response).
bk	Animal \times site response	Similar to “b,” except rather than a global step change, the behavioral response is specific to each detector or site.
Bk	Animal \times site response	Similar to “B,” except rather than a global transient change, the behavioral response is specific to each detector or site.
k	Site learned response	The effectiveness of the detector/site changes once any animal caught. This change persists for the remainder of the study period.
K	Site transient response	The effectiveness of the detector/site changes once any animal caught. This change depends on each preceding occasion.

Appendix B. Summary of wolves radiocollared on Prince of Wales Island, Alaska, June 2012–June 2015.

Wolf ID	Sex	Weight (kg)	Age ^a	Status	Status change	Fate	Pack	Total GPS locations	Pack home range locations
AF430	F	NA	A	Resident (Honker)	Resident (June 2012)	Unreported human-caused	Ratz	6/7/2012–3/29/2013	6/13/2012–3/29/2014
AF270	F	NA	A	Resident		Reported harvest	Honker	6/10/2012–3/3/2013	6/10/2012–3/3/2013
AM310	M	NA	A	Resident (Honker)	Disperser (November 2012)	Unreported human-caused	Honker	6/7/2012–5/30/2015	6/7/2012–11/10/2012
AM260	M	32.5	A	Extraterritorial	Resident (November 2012)	Unreported human-caused	NA	9/22/2012–9/13/2013	NA
AF255	F	30.5	Y	Resident		Reported harvest	Staney	9/25/2012–2/2/2014	9/25/2012–2/2/2014
JF465	F	21.8	J	Resident (Honker)	Disperser (May 2013)	Reported harvest	Honker	9/30/2012–4/19/2015	9/30/2012–5/10/2013
JF495	F	23.3	J	Resident		Reported harvest	Honker	10/11/2012–3/13/2013	10/11/2012–3/13/2013
JM435	M	28	J	Resident		Collar blow-off	Honker	10/23/2013–9/8/2014	10/23/2013–9/8/2014
YM330	M	31	Y	Resident (Honker)	Disperser (November 2014)	Intraspecific strife	Honker	5/4/2013–12/31/2014	5/4/2013–11/11/2014
YF250	F	29.5	Y	Resident		Reported harvest	Staney	5/10/2014–10/27/2014	5/10/2014–10/27/2014
201401	F	31	Y	Disperser	Resident	Alive	Memorial Beach	10/6/2014–5/30/2015	NA
201501	M	36.5	A	Resident	Resident	Alive	Memorial Beach	5/8/2015–5/30/2015	NA

^a Age at time of capture (J = juvenile, Y = yearling, A = adult).

Appendix C. Number of aerial and camera observations used to produce fall (15 August–31 December) minimum counts, Prince of Wales Island, Alaska, 2012–2014.

Pack	Aerial	Camera	Other
2012			
Honker	3	3	0
Ratz	3	0	0
Staney	2	2	0
2013			
Honker	0	7	0
Staney	1	10	0
Sweetwater	0	3	0
2014			
Honker	1	4	0
Memorial Beach	0	0	1 ^a
Staney	0	0	0
Sweetwater	0	3	1 ^a
Total	10	32	2

^a Observed from the ground.

Appendix D. Number of wolf dens checked, active dens, and number of pups observed by wolf pack, Prince of Wales Island, Alaska, 2012–2015.

Year	No. checked	No. active dens	Packs with active dens	Pups observed
2012	4	3	Honker, Ratz	Ratz = 1 ^a
2013	14	2	Honker, Staney	Staney = 5
2014	11	4	Honker, Tuxekan ^b	Honker = 3 and 7 ^c
2015	24	1	Honker	Honker = 1

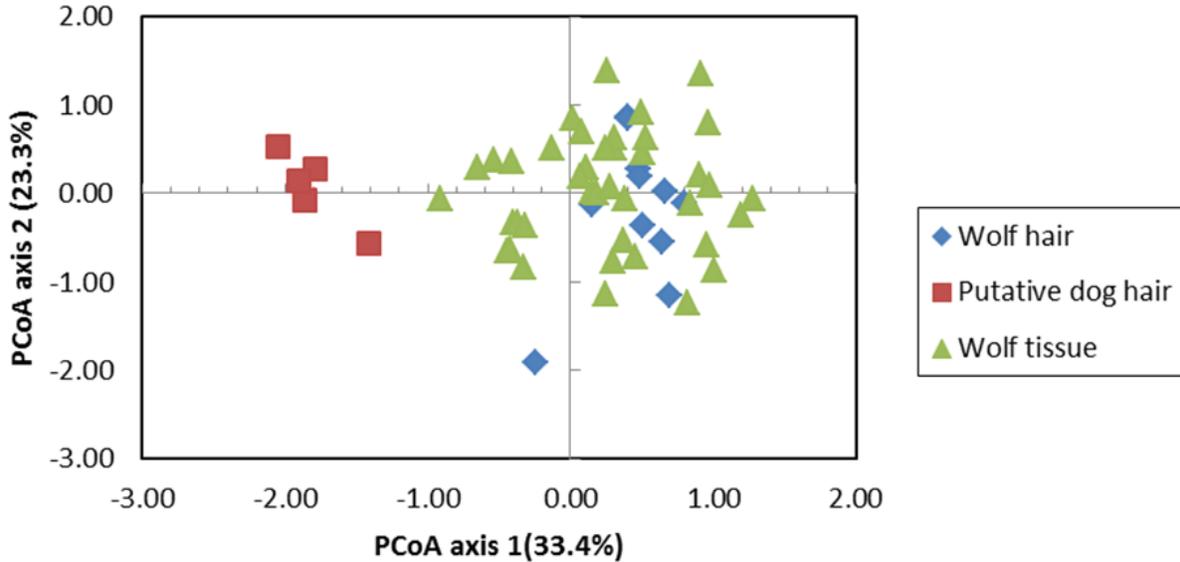
^a Juvenile captured 18 June 2012 and released.

^b Outside of study area.

^c Two active dens were observed in 2014 within the Honker pack home range.

Appendix E. Principal coordinate analysis (PCoA) results.

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 33.4% and 23.3% of the genetic variation, respectively.



Appendix F. Predicting wolf densities from a habitat-derived ungulate biomass index in GMU 2

Prey biomass can be used to indirectly estimate predator abundance, and has been applied to predict wolf densities based on relationships with an ungulate biomass index (UBI) established using research from North American populations (Keith 1983, Fuller 1989, Fuller et al. 2003). Here, we used ungulate biomass regression models to predict wolf densities in wildlife analysis areas (WAAs) in Game Management Unit (GMU) 2 for comparison to wolf densities calculated during 2013–2014 from DNA spatial capture-recapture (SECR) methods.

Estimated habitat suitability index (HSI)-based carrying capacities (number of deer) by WAA were used to calculate indices of ungulate biomass (Fuller et al. 2003). The HSI carrying capacity (USFS 2012) estimates during 1995–2045 (in decadal increments) were generated from habitat capability maps from public and private lands (D. Albert, The Nature Conservancy, 2015, personal communication), and were also used in the Endangered Species Act (ESA) wolf viability models (Gilbert et al. 2015). Changes in habitat capability values during this time period reflect forest succession from clear-cuts to stem exclusion status, and do not represent future timber sales or other forest alterations.

We used an ungulate biomass regression model based on Fuller et al. (2003), and modified by Cariappa et al. 2011 (a quadratic regression model to accommodate the curvilinear relationship). Following Kuzyk and Hatter 2014, we removed 4 data points (Fuller et al. 2003, Table 6.2) from populations (southwestern Manitoba, southcentral Alaska, interior Alaska, and southern Yukon) where wolf densities and ungulate biomass are considered to be independent because human exploitation exceeded 30% (Adams et al. 2008), and 2 populations (northwestern Minnesota and east-central Yukon) where wolves were recolonizing, and thus their densities are not expected to reflect ungulate biomass. Using the quadratic regression model, the relationship between wolf density and ungulate biomass based on 26 North American wolf studies is $y = 5.40x - 0.166x^2$, where $y = \text{wolves}/1,000 \text{ km}^2$ and $x = \text{ungulate biomass}/\text{km}^2$ (Kuzyk and Hatter 2014).

We used the ungulate biomass coefficient of white-tailed deer modified from Fuller et al. 2003 to represent black-tailed deer (0.75; Kuzyk and Hatter 2014). This value was used to convert HSI values to ungulate biomass in GMU 2.

Using the ungulate biomass regression model, estimates of wolf density by WAA ranged from 14.3 to 36.1 wolves/1,000 km² for 2015. The overall predicted wolf density for GMU 2 was 25.3 wolves/1,000 km² for 2015, and ranged between 27.9 wolves/1,000 km² in 1995 to 24.2 wolves/1,000 km² in 2045. The mean wolf density for GMU 2 in 2015 predicted from the regression model (25.3 wolves/1,000 km²) was similar to the wolf density calculated from the top SECR model for fall, 2013 (24.5 wolves/1,000 km², 95% CI = 14.4–41.9 wolves/1,000 km²). The 2013 fall wolf population estimate predicted using SECR models ($\hat{N} = 221$, 95% CI = 130–378) was also comparable to the ungulate biomass regression model ($\hat{N} = 239$); however, the

2014 SECR wolf population estimates were substantially lower. Wolf density in the noninvasive DNA-based study area (Fig. 1) was 9.9 wolves/1,000 km² (95% CI 5.5–17.7 wolves/1,000 km²) and the population estimate for GMU 2 was 89 wolves (95% CI 50–159).

Although many factors can influence wolf abundance, research on North American wolf-prey systems suggest that the availability of ungulate prey is the main limiting factor (Keith 1983, Fuller 1989, Fuller et al. 2003) as indicated by the strong positive relationship with wolf densities and UBI. The 2013 wolf population estimate follows this pattern indicating that wolf populations are responding to availability of ungulate biomass. However, if the wolf population in GMU 2 is largely driven by deer biomass (predicted from the HSI model) we would expect the 2014 population estimate to be closer to the 2013 estimate. Instead it is substantially lower, suggesting some other factor is at play in limiting wolf abundance in GMU 2.

Because availability of vulnerable ungulate prey is difficult to measure (Fuller et al. 2003), ungulate biomass is used as a proxy. In the majority of the North American studies used by Fuller et al. (2003), some direct estimate of ungulate abundance was used to estimate ungulate biomass. In GMU 2, one study has been conducted to count deer abundance through DNA mark-recapture techniques (Brinkman et al. 2011), and deer fecal pellet counts are conducted every couple of years to provide a crude index of deer abundance (McCoy 2011). These efforts have focused on particular watersheds, thus unit-wide estimates are not available. Therefore, at the regional scale, the HSI-based values are used instead as an indirect index of deer abundance. These values were not intended for fine-scale (watershed-level) management decisions, but instead for planning at a landscape level (USFS 2012).

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Appendix G. Noninvasive DNA-based detection rates 2013–2014, Prince of Wales Island, Alaska

	Occasion										Total	Mean ± SD	
	1	2	3	4	5	6	7	8	9	10			
2013													
Animals detected	2	2	1	0	8	1	11	7	1	33		3.7 ± 3.9	
Unique animals detected	2	2	1	0	7	1	5	3	0	21		2.3 ± 2.3	
Repeat detection frequency	13	4	4	0	0	0	0	0	0	21		2.3 ± 4.4	
Cumulative detections	2	4	5	5	12	13	18	21	21	21			
Total detections	2	4	1	0	10	1	17	11	1	47		5.2 ± 6	
Nodes used	36	36	36	3	35	36	36	29	7	254		28.2 ± 13.4	
Mean occasion length (days)	6.9	6.7	7.7	6.0	11.9	6.8	7.0	7.0	15.6	2,009		8.4 ± 3.2	
2014													
Animals detected	3	2	5	3	0	2	4	2	8	29		2.9 ± 2.4	
Unique animals detected	3	1	4	2	0	0	2	0	4	16		1.6 ± 1.6	
Repeat detection frequency	10	2	2	1	1	0	0	0	0	16		1.6 ± 3.1	
Cumulative detections	3	4	8	10	10	10	12	12	16	16		N/A	
Total detections	4	2	5	4	0	3	6	2	10	36		3.6 ± 3.0	
Nodes visited	3	2	5	3	0	2	3	1	8	27		2.7 ± 2.4	
Nodes used	72	72	72	72	72	72	72	72	67	644		64.4 ± 22.3	
Mean occasion length (days)	5.8	6.8	6.9	7	7	7	7.8	6.5	6.5	4,420		6.2 ± 2.2	

