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Source: Wildlife Biology, 2018(1)

Published By: Nordic Board for Wildlife Research

URL: <https://doi.org/10.2981/wlb.00468>

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Wolf space use during denning season on Prince of Wales Island, Alaska

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Wolf *Canis lupus* reproductive success may be enhanced by access to favorable habitat with limited disturbance during denning season. Therefore, protection of den sites can be an important management strategy for maintaining viable wolf populations. On Prince of Wales Island in southeast Alaska, USA, management agencies recommend protection of dens and surrounding home ranges. However, these agencies are concerned current protection buffer sizes might be inadequate to promote pup-rearing success. To inform management decisions regarding buffers surrounding wolf dens, we used wolf GPS collar data during 2012–2016 to quantify core and home range area sizes during denning season. We used an autocorrelated kernel density estimator (AKDE) to calculate the extent of home ranges and fit individual wolf movement models. Breeding wolves used smaller core (AKDE 50% isopleth = 6 km², SD = 4 km²) and home range areas (AKDE 95% isopleth = 57 km², SD = 17 km²) during denning season (15 April–15 June) than non-breeding wolves at active dens (core = 69 km², SD = 45 km²; home range = 252 km², SD = 161 km²). Home ranges for breeding wolves and wolves belonging to a reproductive pack were smaller than non-breeding wolves throughout the pup-rearing period (15 April–31 July). The mean minimum and maximum distance from the core area edge to the active den site (1186–6326 m) varied widely but was smaller for breeding wolves (734–2308 m), and all distances exceeded the existing recommended den buffer distance (366 m). These results underscore the importance of evaluating individual variation in space use when considering management actions intended to protect cooperative breeders or other social carnivores. Wolf managers should recognize the current protection buffer around dens constitutes only a portion of the core area used by breeding wolves, and habitat alterations near den sites may force breeding wolves to use sub-optimal habitat they would normally avoid.

Keywords: *Canis lupus*, wolf, dens, home range, pup rearing

Wolves *Canis lupus* exhibit large variation in home range sizes, which is influenced by many factors including wolf density, prey abundance, habitat quality, reproductive status and season (Fuller et al. 2003, Hinton and Chamberlain 2010, Mattisson et al. 2013, Kittle et al. 2015). During denning season, wolf home ranges are constrained because wolf activity is focused around the den site (Jędrzejewski et al. 2001, Ruprecht et al. 2012). Pups are most vulnerable during the first 6 weeks of life due to reduced mobility (Mech and Boitani 2003, Mills et al. 2008), thus wolves generally locate den sites in areas protected from exposure to disturbance (e.g. human settlements, Sazatornil et al. 2016, Llaneza et al. 2018) or less visible due to landscape features or vegetation cover (Trapp et al. 2008; but see Matteson 1992 and Unger

1999). Den sites have ecological importance because survival of wolf pups is most variable during early denning season through late summer, and this component of reproductive success has a large effect on the demographic trajectory of the population (Harrington and Mech 1982, Ballard et al. 1987, Fuller et al. 2003, Benson et al. 2015). Because wolf pup rearing occurs at these sites, reproductive success may be enhanced by access to favorable habitat with limited disturbance during denning season (Sazatornil et al. 2016) as relocating pups may increase risk of mortality (Ausband et al. 2016). However, other studies indicate that in some circumstances wolves can be tolerant of human disturbance during denning season (Chapman 1977, Thiel et al. 1998), and even relocation of pups as a result of disturbance has not caused a negative impact to reproductive success (Frame et al. 2007). Variability in the degree of tolerance wolves display to disturbance underscores the need for more refined information on space use requirements during the denning season, which could help inform management efforts to minimize anthropogenic disturbance where and when it is necessary.

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Wolves in southeast Alaska have been a focus of conservation efforts since the mid-1990s, triggered by concerns over the negative ecological consequences of old-growth logging on wildlife habitats, increased human-caused wolf mortality facilitated by access via logging roads (Person et al. 1996, Person and Russell 2008, Person and Brinkman 2013), and later by decreases in wolf density on Prince of Wales Island (POW) over the past two decades (Person et al. 1996, Roffler et al. 2016). Conservation concerns have been focused on Prince of Wales Island (POW; Fig. 1), as it is estimated to harbor approximately one third of the southeastern Alaskan wolf population (Person et al. 1996), and also has the highest rates of logging in southeast Alaska with an extensive road system (Albert and Schoen 2013, Person and Brinkman 2013). On three occasions the US Fish and Wildlife Service has conducted 12-month Endangered Species Act reviews (USFWS 1995, 1997, 2016) of the Alexander Archipelago wolf *Canis lupus ligoni*. Although listing was determined to be not warranted for all decisions, the need for improved management of wolf harvest and habitats

was outlined as a critical component to maintaining viable populations of wolves.

The US Forest Service (USFS) manages the majority of southeast Alaska lands and along with the US Fish and Wildlife Service and Alaska Dept of Fish and Game (ADF&G), through the Wolf Technical Committee has recently developed recommendations to maintain sustainable populations of POW wolves (Wolf Technical Committee 2017), a management indicator species in the Tongass National Forest Land and Resource Management Plan (USFS 1997, 2008, 2016). Management recommendations include enhancement of the habitat of POW wolves' primary prey, Sitka black-tailed deer *Odocoileus hemionus sitkensis* through forage enhancement and protecting old-growth forest and restricting human-caused mortality of wolves through management of road access and harvest regulations. A primary recommendation was to protect wolf dens to avoid disruption of reproductive activities. The Wolf Technical Committee was specifically concerned the guidelines in the current Forest Plan to provide a forested

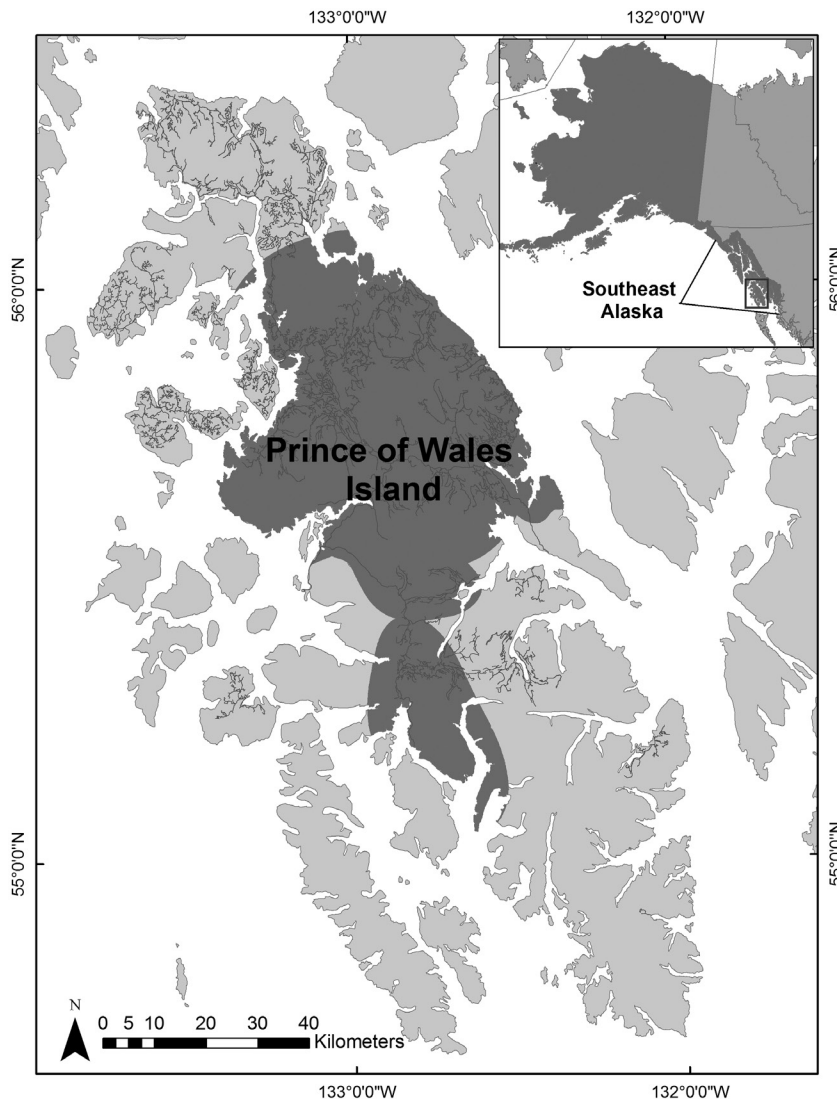


Figure 1. Wolf space use study area, Prince of Wales Island, Alaska, USA, 2012–2016. Composite home range area (combined home ranges of 13 wolves) during the denning period (15 April–15 June) is shown in dark grey, roads shown in black.

buffer around den sites where road construction is discouraged (currently 1200 feet [366 m]) may not be adequate to ensure successful breeding at a den site. In addition, the committee also recommended protecting all documented wolf dens indefinitely, which was a change from only protecting dens that were active (Wolf Technical Committee 2017).

On POW, wolves select den sites in low elevation, flat terrain, in old-growth forests adjacent to open habitats (e.g. meadows and muskegs) and freshwater streams or lakes, and avoid high density road areas (Person and Russell 2009, Roffler et al. 2018). The recently revised management recommendations endorsed permanent protection of den sites and adequate surrounding habitat (where foraging and other activities occur) to allow for pup-rearing success (Wolf Technical Committee 2017), but the Wolf Technical Committee delayed defining specific den buffer distances and the proportion of old-growth habitat (considered to be important for deer and wolf denning habitat; Wallmo and Schoen 1980, Person 2001, Person and Russell 2009) to be maintained within foraging areas pending development of and evaluation of new information. We conducted this research to provide more detailed information to the Wolf Technical Committee regarding den site habitat use of wolves which could be used to better inform protection of den sites.

In this study we assessed wolf den site habitat use and seasonal home range sizes. Our first objective was to quantify the size of core areas around each den site. We conducted these analyses specifically to provide information requested by the Wolf Technical Committee including the maximum and minimum distances from the core area boundary to the den. Our second objective was to quantify the size of home range areas around the den site, and then within each home range to assess habitat characteristics, specifically the proportion of old-growth forest in relation to other land cover categories, and distance of den sites to roads. The third objective of this study was to quantify seasonal (pup-rearing, late summer, fall, late winter) home range sizes of individual wolves and wolf packs, and to examine the relationship between individual home range size and wolf characteristics (individual identity, wolf pack membership, sex, breeding status, association with an active den) and temporal characteristics (season and year). We used wolf GPS collar data collected at shorter intervals than VHF radio collars used in previous wolf research on POW, and thus we were able to assess movement patterns and calculate home ranges during the abbreviated denning season, which were not previously possible. The research will provide information to guide long-term management of wolf den sites in forested environments and ecological insight regarding variation in seasonal space use and behavior.

Material and methods

Study area

Our study area was located on POW, the largest island (6670 km²) in the southeast Alaska Archipelago (Fig. 1). Temperate rainforests dominated by Sitka spruce *Picea sitchensis* and western hemlock *Tsuga heterophylla* are the

major land cover and were interspersed with even-aged forest stands at varying successional stages resulting from clearcut logging. Muskegs, marine estuaries, riparian and alpine zones are non-forest habitat types on POW. Our study area was focused in north-central POW, an area with extensive industrial-scale logging and approximately 4800 km of logging roads (densities in northern POW 0–4.44 km km⁻²; Roffler et al. 2018). Wolf density on POW and the surrounding islands ranged from 39.5 wolves/1000 km² in 1994 to 9.9–25.5 wolves/1000 km² during 2013–2016 (Roffler et al. 2016).

Captures and monitoring

We captured and radiocollared wolves during 2012–2016 using methods described previously in Roffler et al. (2018). Briefly, we used modified padded long spring and unpadded coil spring foothold traps with commercially-produced lures and canid urine used as attractants. Restrained wolves were chemically immobilized (using either tiletamine HCl and zolazepam HCl, or a combination of ketamine and medetomidine) and fitted with a spread-spectrum, GPS radio collar (Mod 4500, Telonics, Inc.). All capture and handling procedures were approved by the State of Alaska Animal Care and Use Committee. The GPS collars obtained a location every 6 h during January–August, and every 2 h September–December, which were thinned to every 6 h for consistency. Collars automatically released after 24 months.

We used GPS location data to detect active den sites. Putative active dens were first identified by examinations of collared wolf locations that were geographically focused in a restricted area during the period of time previously identified as the parturition period (between the last week of April and the second week of May; Person and Russell 2009). We also visited den sites 3–6 weeks after suspected parturition to verify pup production by visual observation. We approached sites on foot in groups of 1–3 people and recorded observations of wolves when they were seen or heard. We searched the area around the den entrances for signs of fresh wolf scat, hair, scrapings or other sign. We observed the den for wolf pups but limited our time in the area to < 1 h to avoid excessive disturbance of breeding wolves. Despite these efforts, 3 wolf packs relocated their pups to a nearby den (<0.5 km) during the study period. In 2 of these cases, additional visits were made by agency employees to the den after our field visits to observe pups, and in one case low-level helicopter flights for logging activities began immediately before the relocation event (Roffler et al. unpubl.). Person and Russell (2009) also reported a low number of relocations in response to human visits to den sites. In addition, we annually visited 26 dens previously recorded by Person and Russell (2009) during 1995–2004, using the same timing and techniques to make observations of wolves at historic dens.

We established remotely triggered motion-detecting cameras at den sites (Reconyx HC600, Reconyx, Inc. Holmen, WI, or Moultrie M990i, Moultrie Products, Alabaster, AL) and reviewed images to verify the presence of pups. Cameras were established 15–30 m from the den. Timing of den occupancy was determined by reviewing the GPS location data. Wolves were considered associated

with a den site during the period of time they had locations consistently (≥ 2 locations within a 5-day moving window) within 200 m of the verified den location. Breeding females were identified visually during handling or in photos from cameras at den sites by evidence of lactation (Mech et al. 1993), or behavior at the den site (e.g. nursing pups, Mech and Boitani 2003). One breeding male was identified as the only male member of the pack and by den site behavior. Non-breeding wolves were adult (≥ 2 years old) members of the pack that did not display evidence of pup-rearing or dominant behavior identified visually from camera photos or observations.

Home range estimation

To determine the area of use around wolf dens, we first examined space use focusing on the early denning period (15 April–15 June), including the parturition period until pups are 6 weeks old. We calculated home ranges for individual wolves and used the 50% contours to define the core area, and 95% contours to define the broader home range around each den site (Benson and Patterson 2015, Hinton et al. 2016).

We then quantified seasonal home range sizes throughout the year of individual wolves and wolf packs using 95% contours. We established four home range seasons based on wolf life history and previous research conducted in the study area (Person and Russell 2009, Roffler et al. 2018). The pup-rearing season (15 April–31 July) encompassed both the denning season and the period of time that wolf packs begin to move to rendezvous sites. During late summer (1 August–14 October) pups become more mobile and the pack activity center shifts to rendezvous sites and salmon spawning areas (Person 2001). Fall (15 October–31 December) is a period of higher mobility as pups and adults make larger movements throughout their home ranges. Late winter (1 January–14 April) includes the breeding season and is also a period of increased territorial behavior (Mech and Boitani 2003). We used data only from resident radiocollared wolves in our analyses, and therefore excluded locations of wolves during extraterritorial forays (temporary movements outside of a home range that are markedly separate from their previous locations; Ballard et al. 1997, Burch et al. 2005), or dispersal (a permanent movement away from the natal pack home range, or did not remain in one home range area for > 14 days; Person and Russell 2008).

We used an autocorrelated kernel density estimator (AKDE; Fleming and Calabrese 2017) to calculate home ranges, conducted using the *ctmm* 0.3.2 package (Calabrese et al. 2016, Fleming and Calabrese 2017) with R ver. 3.3.2 software (<www.r-project.org>). The AKDE method uses a semi-variance approach to account for the inherently autocorrelated nature of relocation data, as locations close together in time are also close together in space. AKDE fits a movement model to the location data to estimate the autocorrelation structure, which is then used to derive the optimal bandwidth. Standard methods that do not account for autocorrelation generally underestimate home range size (Fleming et al. 2015).

Following the steps to create AKDEs outlined in Calabrese et al. (2016) we first visually fit a semi-variogram

function to the variogram of each individual wolf's movement data. We then fit isotropic (general movement patterns) and anisotropic (directional) versions of movement model types appropriate for our location data (independently identically distributed [IID], Ornstein–Uhlenbeck [OU], and Ornstein–Uhlenbeck foraging [OUF]) and selected the top-ranked model via Akaike's information criterion corrected for small sample sizes (AICc) via the *ctmm* function *ctmm.select*. The IID model assumes uncorrelated locations and velocities (equivalent to kernel density estimation), whereas the OU and OUF models describe a tendency of directed movement towards a central location (e.g. the center of a home range). OU and OUF models both describe a restricted space use process (e.g. residency in a home range) but are distinguished in that velocities are uncorrelated with OU, whereas velocity is correlated with OUF (Calabrese et al. 2016). Both the OU and OUF models estimate home range size and the position autocorrelation time, typically interpreted as home range crossing time. We averaged the probability density functions from the utilization distributions of each of the individual radiocollared wolves in a pack to obtain the home range for each pack (C. Fleming pers. comm.).

We also calculated seasonal home ranges for each wolf pack using 95% minimum convex polygons (MCP; Mohr and Stumpf 1966) with the *hr* package (Signer and Balkenhol 2015) in R. We included MCP seasonal home range calculations only for comparisons with previous wolf home range estimates in our study area and elsewhere. All analyses were conducted using AKDE-calculated home ranges. All seasonal home ranges and core use areas were clipped to the shoreline of POW.

Data analyses

Core and denning home range area

We tested for differences in size of core and denning home range areas between 1) breeding wolves, 2) non-breeding wolves associated with an active den, and 3) wolves not associated with an active den using analysis of variance (ANOVA) with Tukey's post hoc tests ($\alpha=0.05$). We lacked a sufficient sample size to test for differences between male and female breeding wolves. To measure core use of denning areas, we measured the shortest and longest distances from the active den site to the edge of the core area polygon for individual wolves associated with the active den site (Fig. 2). We measured straight line distance from all active den sites observed during our study period to the nearest open road. We used ArcMap 10.2.1 (ESRI, Redlands, CA) to conduct all spatial analyses.

To assess the quantity of old-growth habitat within denning season home ranges we calculated the proportion of old-growth forest in relation to other forest and land cover categories. Land cover spatial data development is described in Roffler et al. (2018). Old-growth forest was >150 years old. Medium- and high-volume old-growth forest were combined and evaluated as a separate category from low-volume old-growth forest because they have a higher value to deer as winter habitat (Suring et al. 1993). Young clearcuts were classified as ≤ 30 years since cut, and were characterized by the occurrence of understory shrubs, whereas old clearcuts were classified as > 30 years since cut, with dense canopies

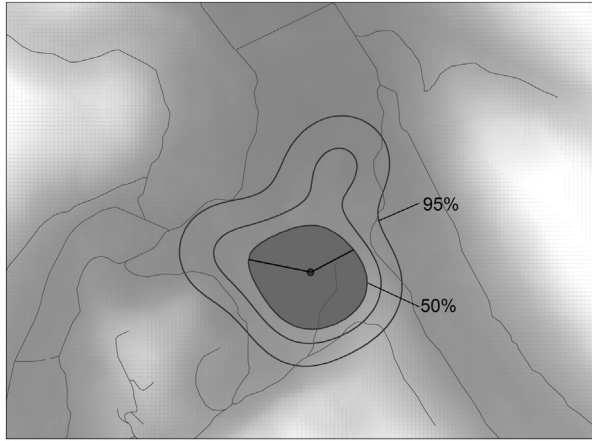


Figure 2. Schematic of core use area (AKDE 50% isopleth) and home range area (AKDE 95% isopleth) estimated with autocorrelated kernel density estimators (AKDE) during denning season (15 April–15 June), Prince of Wales Island, Alaska, USA. The core use areas around dens (gray dot) were quantified by measuring the shortest and longest distances (black lines) from the den site to the edge of the 50% isopleth.

and low occurrence of understory shrubs (Farmer and Kirchhoff 2007). The thinned forest category was comprised of young forest stands (mean age at the time of treatment was 24 years) that had been precommercially treated with thinning over >50% of their area to lower tree density and enhance timber production. Other land cover classifications included in the forage area analyses were open vegetation (meadows, grasslands and muskegs), other non-forest (freshwater, brush, urban areas), and alpine (high elevation, sparse vegetation, rocks and snow). We resampled all GIS data to a 30 m² cell resolution.

We quantified the proportion of each land cover type within each individual wolf's denning season home range area using the Tabulate Area tool in ArcMap. We tested for differences in proportions of home range area land cover among 1) breeding wolves, 2) non-breeding wolves associated with an active den, and 3) wolves not associated with an active den using ANOVA with Tukey's post hoc tests ($\alpha=0.05$).

Seasonal home ranges

We tested for differences in wolf pack home range size across seasons using an ANOVA with Tukey's post hoc tests ($\alpha=0.05$). In addition to examining home ranges at the wolf-pack scale, we also investigated differences in individual seasonal wolf home ranges and movement models. We first calculated the position autocorrelation time, interpreted as the time required to cross the home range (Péron et al. 2017) for each wolf using ctm (Calabrese et al. 2016, Fleming and Calabrese 2017). We then used generalized linear models (GLMs) with gamma distribution errors and a log link function to examine the relationship between individual wolf home range size and wolf characteristics (individual identity, wolf pack membership, sex, breeding status, association with an active den) and temporal characteristics (season and year). We separately examined the relationship between home range size during the pup-rearing season and wolf characteristics. We used Bayesian information criterion

(BIC) to select the top-ranked model and ranked them according to their weights (BIC_w). Additionally, we evaluated the relationship between the best-fitting movement model for each individual wolf and wolf characteristics using multinomial logistic regression. Analyses were conducted using the lme4 (Bates and Sarkar 2006) and nnet (Venables and Ripley 2002) packages with R software.

Results

Captures and monitoring

During 2012–2016 we monitored 13 radiocollared wolves (eight females and five males) in seven packs with 1–5 wolves radiocollared in each pack. On average GPS collars recorded 809 locations ($SD=415$) per wolf, over a time interval of 401 days collar⁻¹. We detected 11 active den sites on POW during the study period, six of which had radiocollared wolves associated with them. Using the GPS data, visual observations on the ground and photos of wolves from the motion-detecting cameras, we identified the breeding and non-breeding collared wolves at the active den sites. Of the 11 den sites we found, 6 (55%) had been previously used during 1995–2003 (Person and Russell 2009). Five dens had no previously recorded use by wolves. Two den sites were used for two consecutive years during our study period.

Home range estimation

Core and denning home range area

During our study period, the mean den entry date was 2 May (range 20 April–21 May) and the mean den exit date was 1 July (range 20 June–21 July). Breeding wolves had earlier start dates of den occupancy (range=20 April–28 April) than non-breeding wolves associated with an active den site (range=9 May–21 May; Supplementary material Appendix 1 Table A1). On average wolves occupied den sites for 59 days ($SD=22.3$, range=35–82, $n=5$).

Denning season core use areas ranged from 3 to 405 km² (mean=107 km², $SD=121$ km²) for all wolves, and there was a statistically significant difference in mean core area sizes among categories of wolves ($F_{2,10}=4.91$, $p=0.033$). The post hoc Tukey test revealed that the mean core area size of breeding wolves (6 km², $SD=4$ km²) and wolves not associated with an active den (206 km², $SD=142$ km²) differed significantly ($p=0.038$; Table 1). The minimum width of the six active den sites to the core use area edge ranged from 53 m to 1654 m, whereas the maximum width ranged from 1815 m to 14 687 m. The core use area width was narrower for breeding wolves at active den sites (mean minimum distance=734 m, $SD=577$; mean maximum distance=2308 m, $SD=500$) reflecting their smaller core use areas (Table 1). Active den sites on POW during our study period ($n=11$) were on average 0.91 km from the nearest road (range=0.17–3.83 km, $SD=1.07$ km).

Home range areas during denning season varied in size from 44 to 1411 km² (mean=376 km², $SD=418$ km²) for all wolves. Similar to the core use area patterns, breeding wolves had a smaller mean home range area (57 km², $SD=10$ km²) in comparison to non-breeding wolves at

Table 1. Wolf core denning area (km²) estimated with 50% autocorrelated kernel density estimators (AKDE) during denning season (15 April–15 June), the minimum and maximum core use area width (m) at active den sites, and number of wolves included in each category (n), Prince of Wales Island, Alaska, USA, 2012–2016.

| | Core denning area (km ²) | | | Core area width (m) | | | |
|--|--------------------------------------|------|-----|---------------------|-------|---------|-------|
| | n | Mean | SD | Minimum | SD | Maximum | SD |
| All wolves | 13 | 107 | 121 | | | | |
| Breeding | 3 | 6 | 4 | 734 | 577 | 2,308 | 500 |
| Active den non-breeding ^a | 5 | 69 | 45 | 1,638 | 1,577 | 10,344 | 6,317 |
| Not associated with an active den ^b | 5 | 206 | 142 | | | | |

^aCore area width is based on non-breeding wolves at active den sites (n = 3).

^bCore area based on home range size of wolves in a pack with no reproduction during denning season.

an active den site (252 km², SD = 161 km²) and wolves not associated with an active den site (691 km², SD = 527 km²) although the difference was not statistically significant ($F_{2,10} = 3.61$, $p = 0.066$; Table 2). The low-volume and high/medium-volume old-growth forest categories made up the largest proportion of land cover within wolf home range areas for all wolves (34 and 28%, respectively, Table 2). The proportion of both old-growth forest categories did not differ significantly among the home range areas of breeding and non-breeding wolves, and wolves associated and not associated with active den sites. The proportion of other land cover types did not differ among wolf groups either, with the exception of old clearcuts which occurred proportionally more in breeding than in non-breeding wolf home range areas during denning season ($F_{2,10} = 10.93$, $p = 0.003$).

Seasonal home ranges

Seasonal home range size varied among packs, with AKDE-calculated home ranges varying from 115 to 922 km² among seasons (Table 3). Wolf pack home range sizes were not significantly different between seasons ($F_{3,21} = 0.25$, $p = 0.895$). Home range size also varied among individuals (mean = 349 km², SD = 260 km², range = 41 km²–1411 km²). The semi-variance function that best fit the wolf location data (top-ranked model via AICc for 32 of 49 individual wolf seasonal home range models) was the anisotropic form of the Ornstein–Uhlenbeck foraging movement

model, with anisotropic Ornstein–Uhlenbeck (n = 13) and isotropic Ornstein–Uhlenbeck foraging models (n = 4) comprising the remainder of top-ranked models. The average time for a wolf to cross the linear extent of its home range (autocorrelation time) was 2.89 days (SD = 2.37), and was less during fall (1.95 days, SD = 0.99) in comparison to the pup-rearing season (3.40 days, SD = 2.61), late summer (3.09 days, SD = 2.71), or late winter (3.32 days, SD = 2.91; Table 4).

Wolf pack membership was the most important variable explaining individual wolf home range sizes across all seasons ($\Delta\text{BIC} = 2.1$ from next top-ranked model, $\text{BIC}_w = 0.736$; Supplementary material Appendix 2 Table A2), whereas pack membership, breeding status, and association with an active den site were the most important variables explaining individual wolf home range size during the pup-rearing season ($\Delta\text{BIC} = 2.54$ from next top-ranked model, $\text{BIC}_w = 0.78$; Supplementary material Appendix 3 Table A3). At the individual wolf level, pup-rearing season home ranges were smaller for wolves associated with an active den site ($\beta = -0.939$, $\text{SE} = 0.236$, $p = 0.016$), and for breeding wolves ($\beta = -0.798$, $\text{SE} = 0.236$, $p = 0.028$; Supplementary material Appendix 4 Table A4). Examination of individual home ranges of wolves during the pup-rearing season revealed breeding wolves had smaller home range sizes (mean = 165 km²) than non-breeding wolves (mean = 459 km²; $t_{11} = -2.19$, $\text{df} = 10.9$, $p = 0.051$).

Table 2. Mean and standard deviation (\bar{x} [SD]) of wolf home range areas (km²) estimated across each category with 95% autocorrelated kernel density estimators (AKDE) during denning season (15 April–15 June), the number of wolves included in each category (n), and the mean and standard deviation (\bar{x} [SD]) of the proportion of each land cover category in the home range areas, Prince of Wales Island, Alaska, USA, 2012–2016.

| | All wolves | Breeding | Active den non-breeding | Not associated with an active den |
|--------------------------------------|--------------|--------------|-------------------------|-----------------------------------|
| n | 13 | 3 | 5 | 5 |
| Home range area (km ²) | 376 (418) | 57 (17) | 252 (161) | 691 (527) |
| High/medium-volume old-growth forest | 0.28 (0.068) | 0.32 (0.010) | 0.29 (0.084) | 0.25 (0.066) |
| Low-volume old-growth forest | 0.34 (0.069) | 0.26 (0.046) | 0.35 (0.068) | 0.36 (0.054) |
| Young CC ^a | 0.09 (0.049) | 0.13 (0.012) | 0.04 (0.023) | 0.11 (0.015) |
| Old CC ^b | 0.10 (0.076) | 0.19 (0.012) | 0.07 (0.068) | 0.12 (0.069) |
| Thinned ^c | 0.09 (0.045) | 0.07 (0.030) | 0.11 (0.046) | 0.08 (0.051) |
| Open ^d | 0.02 (0.013) | 0.01 (0.023) | 0.02 (0.011) | 0.01 (0.009) |
| Other non-forest ^e | 0.08 (0.088) | 0.01 (0.006) | 0.11 (0.123) | 0.09 (0.053) |
| Alpine ^f | 0.01 (0.014) | 0.00 (0.000) | 0.02 (0.021) | 0.00 (0.005) |

^a≤30 years since clearcut.

^b>30 years since clearcut.

^c≥ 50% of forest stands were precommercially treated.

^dmeadows, grasslands and muskegs.

^efreshwater, brush, urban areas.

^fhigh elevation, sparse vegetation, rocks and snow.

Table 3. Monitoring period by pack and season (pup-rearing: 15 April–31 July, late summer: 1 August–14 October, fall: 15 October–31 December, and late winter: 1 January–14 April), and wolf pack home range size (km²) estimated with minimum convex polygons (MCP) and autocorrelated kernel density estimators (AKDE), Prince of Wales Island, Alaska, USA, 2012–2016.

| Pack | Monitoring period | Home range size (km ²) | |
|--------------------|-------------------|------------------------------------|-----------|
| | | MCP | AKDE |
| Pup-rearing | | | |
| Honker | 2012–2014 | 516 | 922 |
| Hydaburg | 2013 | 168 | 211 |
| Nossuk | 2013 | 375 | 585 |
| Ratz | 2012 | 100 | 251 |
| Sandy Beach | 2015–2016 | 265 | 241 |
| Staney | 2012–2015 | 110 | 145 |
| Trocadero | 2016 | 116 | 217 |
| Mean (SD) | | 236 (159) | 394 (283) |
| Late summer | | | |
| Honker | 2012–2014 | 363 | 356 |
| Hydaburg | 2013 | 180 | 220 |
| Nossuk | 2013 | 375 | 533 |
| Ratz | 2012 | 392 | 840 |
| Sandy Beach | 2015 | 195 | 292 |
| Staney | 2013–2014 | 131 | 157 |
| Trocadero | – | – | – |
| Mean (SD) | | 273 (116) | 400 (252) |
| Fall | | | |
| Honker | 2012–2014 | 687 | 558 |
| Hydaburg | 2013 | 183 | 161 |
| Nossuk | 2013 | 465 | 545 |
| Ratz | 2012 | 450 | 249 |
| Sandy Beach | 2015 | 324 | 115 |
| Staney | 2012–2013 | 257 | 268 |
| Trocadero | – | – | – |
| Mean (SD) | | 394 (180) | 316 (191) |
| Late winter | | | |
| Honker | 2012–2014 | 730 | 772 |
| Hydaburg | – | – | – |
| Nossuk | 2012 | 447 | 533 |
| Ratz | 2012 | 312 | 219 |
| Sandy Beach | 2014–2015 | 122 | 133 |
| Staney | 2012–2014 | 128 | 120 |
| Trocadero | 2016 | 565 | 917 |
| Mean (SD) | | 384 (243) | 449 (344) |

The best-fitting movement model contained sex and breeding status as explanatory variables ($\Delta\text{BIC}=6.62$ from next top-ranked model, $\text{BIC}_w=0.963$). In comparison to the most common movement model (the anisotropic form of the OUF, for 32 of 49 individual wolf home range models), females were more likely to conform to the OU anisotropic model than males ($\beta=2.140$, $\text{SE}=1.128$, $p=0.057$) and

Table 4. Mean and standard deviation (SD) of seasonal (pup-rearing: 15 April–31 July, late summer: 1 August–14 October, fall: 15 October–31 December, and late winter: 1 January–14 April) individual wolf home ranges (km²) estimated with 95% autocorrelated kernel density estimators (AKDE), mean and SD of home range crossing times (days), and number of individual seasonal wolf home ranges (n), Prince of Wales Island, Alaska, USA, 2012–2016.

| | n | Home range | | Home range crossing time | |
|--------------------|----|------------|-----|--------------------------|------|
| | | Home range | SD | SD | SD |
| Pup-rearing season | 13 | 391 | 352 | 3.4 | 2.61 |
| Late summer | 12 | 337 | 207 | 3.09 | 2.71 |
| Fall | 14 | 270 | 169 | 1.95 | 0.99 |
| Late winter | 10 | 419 | 292 | 3.32 | 2.92 |

breeders were more likely to conform to the OU anisotropic model ($\beta=2.303$, $\text{SE}=1.189$, $p=0.052$). Indeed, of the 13 individual wolf home range models conforming to this movement model, 12 were female home range models, and included all of the wolves that were documented as breeding. The isotropic OUF model represented all females of non-breeding status, whereas the anisotropic OUF consisted of both non-breeding males and females.

Discussion

Evaluation of core use area during denning season

The objectives of the revised den management recommendations included permanent protection of den sites, maintaining sufficient habitat and activity buffers around dens to buffer wolves from development and human activity, and retaining sufficient old-growth forest in foraging areas for pup-rearing. The area surrounding wolf dens required for protection has been proposed in other systems and varies depending on the magnitude and timing of the potential disturbance, the quality of the surrounding habitat matrix, and the legal status of the wolf population. For example, buffers of 1.6–10 km have been recommended to reduce disturbance surrounding den sites in British Columbia, the Canadian and US Rocky Mountains, and interior Alaska (Chapman 1977, Matteson 1992, Fritts et al. 1994, Paquet and Darimont 2002) and were determined from observations of wolf behavior and habitat characteristics of den sites. The current buffer recommendations in the Tongass National Forest Land and Resource Management Plan (366 m; USFS 1997, 2008, 2016) are considerably smaller and believed to be sufficient for wolves during denning season to prevent relocations of pups to another den site in response to noise from ground-based timber harvest activities and other disturbance in forested habitats due to noise attenuation (Wolf Technical Committee 2017). For louder activities such as helicopter overflights and road construction, a buffer of 805 m (0.5 mile) was recommended. The rationale used to establish the 366 m buffer distance was unspecified (D. Person pers. comm.) highlighting the importance of transparently defining justification for management criteria, and the specific information required to meet these criteria.

Our research quantified core use areas to inform management efforts to protect dens from disturbance by using empirical data to describe wolf space use and movement patterns. Although we did not specifically evaluate wolf tolerance of human disturbance, we believe that these data reflect habitat and space requirements around active den sites during the denning period when pups are most vulnerable. Based on our results, the current recommend buffer does not encompass denning use areas. Despite breeding wolves having smaller core use areas (and corresponding den buffer widths), the mean distance of the edge of their core home range from the active den still exceeded the current recommended forest buffer distance (366 m) around the den site by nearly 2 (734 m) to more than 6 times (2308 m). When considering the non-breeding pack members associated with an active den site, the mean core home range edge further exceeded the buffer distance recommended for both

ground-based disturbance (by a minimum of 1272 m) and louder noises (by a minimum of 833 m).

Protection of breeding wolves during the early denning season is an essential step to ensure reproductive success and population viability; however, because wolves are cooperative breeders it is also important to consider the requirements of the non-breeding members of the wolf pack. These wolves play an important role in both attending and provisioning the pups especially before weaning due to reduced mobility of the breeding female (Ballard et al. 1991, Potvin et al. 2004, Ruprecht et al. 2012). Conversely, because they are not as closely tied to the den site, these wolves may be better able to cope with disturbance. Inspection of individual wolf home ranges in our study revealed much variation in home range size, with breeding status emerging as the major influencing factor. As has been documented in other wolf populations, reproductive status influences space use as breeding wolves travel shorter distances, are less active, and have higher den attendance rates than non-breeding wolves (Theuerkauf et al. 2003, Potvin et al. 2004) translating to smaller home ranges for the breeding pair than non-breeding pack members (Hinton and Chamberlain 2010). These results underscore the importance of evaluating space use in terms of individual characteristics, as individual variation can be obscured when evaluating home range size at the pack level.

Home range area and habitat during denning season

The extent of home range areas was also variable during denning season and mainly influenced by breeding status, with smaller home range areas for breeding than non-breeding wolves. As breeding status influenced individual variation in core and home range sizes during denning season, movement patterns also varied according to this factor. Breeding females conformed to the OU anisotropic movement model indicating that they displayed discontinuous velocity and tortuous movements relative to other wolves, particularly during the pup-rearing season and late summer. Breeding females have high attendance rates at dens especially postparturition (Ballard et al. 1991, Potvin et al. 2004, Ruprecht et al. 2012), and maintaining close proximity to den sites could provide an explanation for convoluted movement patterns resulting in irregular speed. In contrast, the majority of the non-breeding wolves (which have variable attendance rates at den sites) in our study, displayed foraging movement patterns (OUF) indicating continuous velocity and directional movement. Space used shifted during fall as all wolves (regardless of breeding status) took less time to cross their fall home ranges than during other times of the year, coinciding with the period when pups become more mobile and movements patterns radiating from a den or rendezvous site are no longer necessary.

The quantity of each land cover category in the home range areas during denning season was mostly proportional to the land cover quantities within the greater study area (north-central POW, Fig. 1), with old-growth forest making up the majority of the home range areas, and other non-forest, clearcuts, treated forest, and open vegetation occurring in declining quantities (Table 1, Roffler et al. 2018). Therefore, the habitat quality within home range areas

during denning season reflected the existing habitat at the landscape scale. There was little variation in the proportions of land cover categories based on breeding-status or association with an active den site indicating that breeding status was more influential to the overall quantity of area used by an individual rather than the quality of the habitat. One notable exception was a higher proportion of old clearcut forest in the home range areas of breeding wolves during denning season. Previous habitat selection research demonstrates that wolves avoid old and young clearcuts during denning season despite proximity and inclusion within the home range (Person and Russell 2009, Roffler et al. 2018). During this study den sites were generally located in old-growth forest, corroborating previous results (Person and Russell 2009), but examination of the surrounding landscape revealed the occurrence of old clearcut forests sometimes in close proximity to den sites (0.1–1 km). This pattern of den site selection reflected hierarchical habitat selection demonstrated in some wolf populations wherein wolves select a territory and within it the most favorable habitat for den sites to reduce risk (Trapp et al. 2008, Szatornil et al. 2016).

Differences in the proportion of old clearcut forest in denning home ranges may be explained by variation in movement patterns. Breeding wolves, due to their restricted mobility may be unable to use more old growth forested habitat because it would necessitate greater travel distances from the den site. In contrast non-breeding wolves had home range areas approximately 8 times larger than breeding wolves and therefore a greater ability to incorporate more old-growth forest into their home ranges despite the proximity of unfavorable habitat (i.e. clearcuts). Of note is that clearcuts were avoided within denning season home ranges during 1995–2004 (Person and Russell 2009) and during 2012–2016 (Roffler et al. 2018), all the while becoming a more common land cover category.

During our study period over half of the den sites ($n=6$) had been used previously during 1995–2003. The consistent reuse of these historic den sites by wolves could be due to variety of factors including learned behavior, or a limitation in availability of favorable denning habitat. However, the ability of wolves to establish new den sites ($n=5$) was also documented during this study indicating some degree of flexibility in den site selection, sufficient availability of den habitat, or both. Due to demonstrated use of historic den sites with recorded denning activity up to 17 years previously, and reuse of den sites during this and earlier research (Person and Russell 2009), the Interagency Wolf Habitat Management Program recommended changes to the Forest Plan to indefinitely protect known den sites (instead of only for active dens) are supported.

Seasonal home range and movement patterns

Overall, there was a great deal of variability in wolf seasonal home range size and space use throughout the year, with differences explained more by wolf pack membership than by seasons. Home range sizes are negatively related to habitat quality (Kittle et al. 2015), prey density (Fuller 1989, Mattisson et al. 2013, Lake et al. 2015), and wolf density (Peterson et al. 1984, Ballard et al. 1987), and can also be influenced by pack composition (Tallents et al. 2012), ter-

rain features, and harvest (Rich et al. 2012). One pack in our study (the Honker pack) had larger pup-rearing home ranges than those of other packs (Table 3). There was evidence of multiple breeding females in the Honker pack during late May–mid July 2014, as radiocollared wolves, unmarked adults and pups were observed at two den sites 8 km apart. Occurrence of multiple breeding females in wolf packs is not common (6–8% of all packs; Mech 2000, 15.8% of all packs Ausband 2018), but could have contributed to the larger pup-rearing home range size of this pack (Table 3). Turnover of the breeding female is associated with the occurrence of multiple breeding females in a pack (Ausband et al. 2017). Additionally, the Ratz pack budded from the Honker wolves in 2012 and occupied an adjacent territory for 10 months but made occasional forays after the pup-rearing season into the Honker home range. This pattern is consistent with budding events documented elsewhere with overlap of the new and the originating pack home ranges, although overlap is lowest during the early denning season (Jędrzejewski et al. 2004). The budding event also contributed to the partly larger late summer and fall home range sizes of the Honker and Ratz packs relative to other packs in the study area (Table 3).

Seasonal pack home range sizes did not vary as much throughout the year as previously reported (Person 2001). Similar home range sizes between the pup-rearing period and late winter have been more commonly documented (Potvin et al. 1988, Fuller 1989) and are attributed in part to lower pack cohesion (Metz et al. 2011) and rotational foraging patterns (Demma and Mech 2009) during summer. Seasonal pack home range sizes were also larger than those previously reported (Person 2001), which were calculated using both MCPs and kernel density estimators (KDEs). This could be due to either methodological or ecological factors. Our study used GPS radiocollars, whereas Person (2001) used VHF radiocollar data collected at longer time intervals (every 5–14 days) to determine home range size. Rarefaction of our location data to assess the effects of less frequent position fixes on home range size resulted in MCP home ranges that were ~30% smaller and KDE home ranges that were 10–25% larger than our position fix rate (ADF&G unpubl.). However, we also used a method to account for spatial autocorrelation; therefore, due to the underestimation of home range size from standard methods (such as KDEs; Fleming et al. 2015), we would expect the AKDEs to be larger. Because home range sizes have an inverse relationship with habitat quality, prey biomass, and wolf density (Ballard et al. 1987, Fuller et al. 2003, Kittle et al. 2015), the larger home range sizes we reported could also be due to ecological factors, including a decrease in wolf density on POW over the past two decades (Person et al. 1996, Roffler et al. 2016), or ecological changes affecting prey density such as reductions of high-quality winter deer habitat (i.e. low elevation old-growth forests).

Management implications

The intent of the Wolf Technical Committee is to provide recommendations to maintain the integrity, attractiveness, and productivity of den sites with forested buffers which will be perpetually protected. The median value of the minimum and maximum distance between the core home range edge

and a den site was 3756 m for all wolves associated with an active den. Therefore, land managers working to protect den sites should consider expanding the much smaller guideline den site buffers in place now to this larger size. The shape of the protected polygon surrounding the den should be selected to maximize high quality denning habitat (flat, low elevation terrain, in old-growth forests, near freshwater and distant from high density road areas, Person and Russell 2009, Roffler et al. 2018). Therefore, the buffer width may vary to accommodate high-priority habitat but should not be less than 734 m (the minimum buffer width for breeding wolves). To maintain foraging habitat for wolves during denning season, it is recommended the proportion of old-growth forest should not be reduced below the current values (61% of the core home range area for wolves associated with an active den). The timing of the restrictions to activities that could cause disturbance is a key consideration; restrictions could be loosened as pups become more mobile (> 6 weeks old) and able to respond to disturbances (Frame et al. 2007). The recommended period for seasonal management activity restrictions around active dens is 15 March–15 July based on earlier work by Person and Russell (2009; Wolf Technical Committee 2017); however, wolves were documented during this study at dens as late as 21 July, and the mean den occupancy was nearly two months, thus extending the restriction period to late July would be a conservative management action. Because wolves display a flexible response to road density throughout the year by avoiding areas with high road densities during denning season, but selecting these areas during winter (Roffler et al. 2018), timing is also a consideration in road closures as a management action. Considering the pattern of repeated historical den site and habitat use, measures to maintain old-growth habitats surrounding documented den sites will help maintain the potential for successful wolf reproduction.

Acknowledgements – We are grateful to D. Person for his foundational POW wolf research. For fieldwork and project assistance, we thank T. Bentz, S. Bethune, G. Blundell, K. Larson, B. Porter, J. Terenzi, R. Slayton, J. Whitman, L. Whitman and K. Zarn. We thank B. Bennetsen, S. Brockmann, A. Crupi, B. Darr, L. Decker, R. Flynn, D. Martin, T. Schumacher and R. Scott who dedicated much effort to establish management guidelines for POW wolves. D. Doyon was instrumental in conducting timely and safe radiotracking flights. B. Dale, C. Krenz, H. Pedersen, T. Schumacher and S. Woodruff provided helpful comments on early drafts of the manuscript.

Funding – This work was funded by the Pittman-Robertson Federal Aid in Wildlife Restoration Program (Project 14.30), the State of Alaska general funds, Cooperative Endangered Species Conservation Fund (Section 6 of the Endangered Species Act) Grant Program (project E-19-1-1), and the US Forest Service, Tongass National Forest.

Permits – All capture and handling procedures were approved by the State of Alaska Animal Care and Use Committee.

References

- Albert, D. M. and Schoen, J. W. 2013. Use of historical logging patterns to identify disproportionately logged ecosystems within temperate rainforests of southeastern Alaska. – *Conserv. Biol.* 27: 774–784.

- Ausband, D. E. 2018. Multiple breeding individuals within groups in a social carnivore. – *J. Mammal.* 99: 836–844.
- Ausband, D. E. et al. 2016. Dog days of summer: influences on decision of wolves to move pups. – *J. Mammal.* 97: 1282–1287.
- Ausband, D. E. et al. 2017. Effects of breeder turnover and harvest on group composition and recruitment in a social carnivore. – *J. Anim. Ecol.* 86: 1094–1101.
- Ballard, W. B. et al. 1987. Ecology of an exploited wolf population in south-central Alaska. – *Wildl. Monogr.* 98: 3–54.
- Ballard, W. B. et al. 1991. Den site activity patterns of gray wolves, *Canis lupus*, in south central Alaska. – *Can. Field-Nat.* 105: 497–504.
- Ballard, W. B. et al. 1997. Ecology of wolves in relation to a migratory caribou herd in northwest Alaska. – *Wildl. Monogr.* 135: 3–47.
- Bates, D. and Sarkar, D. 2006. lme4: linear mixed-effects modeling using Eigen and Eigen. – R package, ver. 2.15.3.
- Benson, J. F. and Patterson, B. R. 2015. Spatial overlap, proximity, and habitat use of individual wolves within the same packs. – *Wildl. Soc. Bull.* 39: 31–40.
- Benson, J. F. et al. 2015. Resource selection by wolves at dens and rendezvous sites in Algonquin park, Canada. – *Biol. Conserv.* 182: 223–232.
- Burch, J. W. et al. 2005. Evaluation of wolf density estimation from radiotelemetry data. – *Wildl. Soc. Bull.* 33: 1225–1236.
- Calabrese, J. M. et al. 2016. ctmm: an R package for analyzing animal relocation data as a continuous-time stochastic process. – *Methods Ecol. Evol.* 7: 1124–1132.
- Chapman, R. C. 1977. The effects of human disturbance on wolves (*Canis lupus*). – MSc thesis, Univ. of Alaska, Fairbanks.
- Demma, D. J. and Mech, L. D. 2009. Wolf use of summer territory in northeastern Minnesota. – *J. Wildl. Manage.* 73: 380–384.
- Farmer, C. J. and Kirchoff, M. D. 2007. Ecological classifications of deer habitat in the Tongass National Forest, Alaska. – *Northwest. Nat.* 88: 73–84.
- Fleming, C. H. and Calabrese, J. M. 2017. A new kernel density estimator for accurate home-range and species-range area estimation. – *Methods Ecol. Evol.* 8: 571–579.
- Fleming, C. H. et al. 2015. Rigorous home range estimation with movement data: a new autocorrelated kernel density estimator. – *Ecology* 96: 1182–1188.
- Fritts, S. H. et al. 1994. The relationship of wolf recovery to habitat conservation and biodiversity in the northwestern United States. – *Landscape Urban Plan.* 28: 23–32.
- Frame, P. F. et al. 2007. Response of wolves to experimental disturbance at homesites. – *J. Wildl. Manage.* 71: 316–320.
- Fuller, T. K. 1989. Population dynamics of wolves in north-central Minnesota. – *Wildl. Monogr.* 105: 3–41.
- Fuller, T. K. et al. 2003. Wolf population dynamics. – In Mech, L. D. and Boitani, L. (eds), *Wolves: behavior, ecology, and conservation*. Univ. of Chicago Press, pp. 161–191.
- Harrington, F. H. and Mech, L. D. 1982. Patterns of homesite attendance in two Minnesota wolf packs. – In: Harrington, F. H. and Paquet, P. C. (eds), *Wolves of the world: perspectives of behavior, ecology and conservation*. Noyes Publications, Park Ridge, pp. 81–105.
- Hinton, J. W. and Chamberlain, M. J. 2010. Space and habitat use by a red wolf pack and their pups during pup-rearing. – *J. Wildl. Manage.* 74: 55–58.
- Hinton, J. W. et al. 2016. Space use and habitat selection by resident and transient red wolves (*Canis rufus*). – *PLoS One* 11(12): e0167603.
- Jędrzejewski, W. et al. 2001. Daily movements and territory use by radio-collared wolves (*Canis lupus*) in Białowieża Primeval Forest in Poland. – *Can. J. Zool.* 79: 1993–2004.
- Jędrzejewski, W. et al. 2004. The process of a wolf pack splitting in Białowieża Primeval Forest, Poland. – *Acta Theriol.* 49: 275–280.
- Kittle, A. M. et al. 2015. Wolves adapt territory size, not pack size to local habitat quality. – *J. Anim. Ecol.* 84: 1177–1186.
- Lake, B. C. et al. 2015. Wolf (*Canis lupus*) winter density and territory size in a low biomass moose (*Alces alces*) system. – *Arctic* 68: 62–68.
- Llaneza, L. et al. 2018. The importance of fine-scale breeding site selection patterns under a landscape-sharing approach for wolf conservation. – *Biodivers. Conserv.* 27: 1239–1256.
- Matteson, M. Y. 1992. Denning ecology of wolves in northwest Montana and southern Canadian Rockies. – MSc thesis, Univ. of Montana.
- Mattisson, J. et al. 2013. Home range size variation in a recovering wolf population: evaluating the effect of environmental, demographic, and social factors. – *Oecologia* 173: 813–825.
- Mech, L. D. 2000. Leadership in wolf, *Canis lupus*, packs. – *Can. Field-Nat.* 114: 259–263.
- Mech, L. D. and Boitani, L. 2003. *Wolves, behavior, ecology and conservation*. – Univ. of Chicago Press.
- Mech, L. D. et al. 1993. Wolf nipple measurements as indices of age and breeding status. – *Am. Midl. Nat.* 129: 266–271.
- Metz, M. C. et al. 2011. Effect of sociality and season on gray wolf (*Canis lupus*) foraging behavior: implications for estimating summer kill rate. – *PLoS One* 6(3): e17332.
- Mills, K. J. et al. 2008. Direct estimation of early survival and movements in eastern wolf pups. – *J. Wildl. Manage.* 72: 949–954.
- Mohr, C. O. and Stumpf, W. A. 1966. Comparison of methods for calculating areas of animal activity. – *J. Wildl. Manage.* 30: 293–304.
- Paquet, P. C. and Darimont, C. 2002. Yeo Island wolf home site recommendation: a proposed solution to the potential conflict between the home site requirements of wolves and areas targeted for timber harvest. – The Heiltsuk Nation, Western Forest Products, Raincoast Conserv. Soc.
- Péron, G. et al. 2017. Periodic continuous-time movement models uncover behavioral changes of wild canids along anthropization gradients. – *Ecol. Monogr.* 87: 442–456.
- Person, D. K. 2001. Alexander Archipelago wolves: ecology and population viability in a disturbed, insular landscape. – PhD thesis, Univ. of Alaska Fairbanks.
- Person, D. K. and Russell, A. L. 2008. Correlates of mortality in an exploited wolf population. – *J. Wildl. Manage.* 72: 1540–1549.
- Person, D. K. and Russell, A. L. 2009. Reproduction and den site selection by wolves in a disturbed landscape. – *Northwest Sci.* 83: 211–224.
- Person, D. K. and Brinkman, T. J. 2013. Succession debt and roads. – In: Orians, G. H. and Schoen, J. W. (eds), *North Pacific temperate rainforests*. Univ. of Washington Press, pp. 143–167.
- Person, D. K. et al. 1996. The Alexander Archipelago wolf: a conservation assessment. – Gen. Tech. Rep. PNW-GTR-384. Portland, OR / US Dept of Agric., Forest Service, Pacific Northwest Res. Stn.
- Peterson, R. O. et al. 1984. Wolves of the Kenai Peninsula, Alaska. – *Wildl. Monogr.* 88: 3–52.
- Potvin, F. et al. 1988. Wolf diet and prey selectivity during two periods for deer in Quebec: decline versus expansion. – *Can. J. Zool.* 66: 1274–1279.
- Potvin, M. J. et al. 2004. Wolf homesite attendance patterns. – *Can. J. Zool.* 82: 1512–1518.
- Rich, L. N. et al. 2012. Anthropogenic mortality, intraspecific competition, and prey availability influence territory sizes of wolves in Montana. – *J. Mammal.* 93: 722–731.

- Roffler, G. H. et al. 2016. Wolf population estimation on Prince of Wales Island, southeast Alaska: a comparison of methods. Final Wildlife Res. Rep., ADF&G/DWC/WRR-2016-1. – Alaska Dept of Fish and Game, Juneau, AK.
- Roffler, G. H. et al. 2018. Resource selection by coastal wolves reveals the seasonal importance of seral forest and suitable prey habitat. – *For. Ecol. Manage.* 409: 190–201.
- Ruprecht, J. S. et al. 2012. Homesite attendance based on sex, breeding status, and number of helpers in gray wolf packs. – *J. Mammal.* 93: 1001–1005.
- Sazatornil, V. et al. 2016. The role of human-related risk in breeding site selection by wolves. – *Biol. Conserv.* 201: 103–110.
- Signer, J. and Balkenhol, N. 2015. Reproducible home ranges (rhr): a new, user-friendly R package for analyses of wildlife telemetry data. – *Wildl. Soc. Bull.* 39: 358–363.
- Suring, L. H. et al. 1993. Model habitat capability model for Sitka black-tailed deer in southeast Alaska: winter habitat. – In: Suring, L. H. (ed.), *Habitat capability models for wildlife in southeast Alaska*. USDA Forest Service, Alaska Region, Juneau, AK, pp. L-1–L-85.
- Tallents, L. A. et al. 2012. Territory quality determines social group composition in Ethiopian wolves *Canis simensis*. – *J. Anim. Ecol.* 81: 24–35.
- Theuerkauf, J. et al. 2003. Daily patterns and duration of wolf activity in the Białowieża Forest, Poland. – *J. Mammal.* 84: 243–253.
- Thiel, R. P. et al. 1998. Tolerance by denning wolves, *Canis lupus*, to human disturbance. – *Can. Field-Nat.* 112: 340–342.
- Trapp, J. R. et al. 2008. Wolf, *Canis lupus*, den site selection in the Rocky Mountains. – *Can. Field-Nat.* 122: 49–56.
- Unger, D. 1999. A multi-scale analysis of timber wolf den and rendezvous site selection in northwestern Wisconsin and east-central Minnesota. – MSc thesis, Univ. of Wisconsin, Stevens Point.
- USFWS [U.S. Fish Wildlife Service] 1995. Endangered and threatened wildlife and plants; 12-month finding for a petition to list the Alexander Archipelago wolf as threatened. – 60 Federal Register 10056, USFWS, Anchorage, AK, USA.
- USFWS [U.S. Fish Wildlife Service] 1997. Endangered and threatened wildlife and plants; 12-month finding on a petition to list the Alexander Archipelago wolf as an endangered or threatened species. – 62 Federal Register 46709, USFWS, Anchorage, AK, USA.
- USFWS [U.S. Fish Wildlife Service] 2016. Endangered and threatened wildlife and plants; 12-month finding on a petition to list the Alexander Archipelago wolf as an endangered or threatened species. – 81 Federal Register 435, USFWS, Anchorage, AK, USA.
- USFS [US Forest Service] 1997. Tongass land management plan revision. – US Dept of Agric. For. Serv. R10-MB-338b, <www.fs.usda.gov/detail/tongass/landmanagement/planning/?cid=stelprdb5445359>, accessed on 1 September 2015.
- USFS [US Forest Service] 2008. Tongass land management plan. – US Dept of Agric. For. Serv. R10-MB-603b, Juneau. url: <https://fs.usda.gov/Internet/FSE_DOCUMENTS/stelprdb5367422.pdf>, accessed on 1 September 2015.
- USFS [U.S. Forest Service] 2016. Tongass land management plan. – US Dept Agric. For. Serv. R10-MB-769j, Juneau. <https://fs.usda.gov/Internet/FSE_DOCUMENTS/fsprdr527907.pdf>, accessed on 1 March 2018.
- Venables, W. N. and Ripley, B. D. 2002. *Modern applied statistics with S*, 4th edn. – Springer.
- Wallmo, O. C. and Schoen, J. W. 1980. Response of deer to secondary forest succession in southeast Alaska. – *For. Sci.* 26: 448–462.
- Wolf Technical Committee 2017. Interagency wolf habitat management program: recommendations for Game Management Unit 2. Management Bulletin R10-MB-822. – USDA For. Serv., USDI Fish and Wildlife Service, and Alaska Dept of Fish and Game.

Supplementary material (available online as Appendix wlb-00468 at <www.wildlifebiology.org/appendix/wlb-00468>). Appendix 1–4.