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Factors influencing Arctic brown bear annual home range sizes and limitations of home range analyses

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Abstract: Home range size is a basic ecological index related to individual's realized niche. Its size can be influenced by body size, sex, maternal status, population density, habitat productivity, spatio-temporal variation of resources, climate, predation risk, and disturbance. Home range estimation can also be greatly affected by methodology and sampling regime. We used Global Positioning System collar data to assess what factors influenced the size of annual home ranges (space use during a single active season) of 28 female and 8 male brown bears (*Ursus arctos*) that denned in the Brooks Range of northcentral Alaska, USA, from 2014 to 2017. We used 2 methods to estimate annual home ranges, the Kernel Density Estimate (KDE) and the dynamic Brownian Bridge Movement Model (dBBMM). Contrary to expectations, we did not find that larger bodied bears of the same sex had larger annual home ranges. Annual home ranges of male bears (mean [standard deviation]; 504 [312] km² and 3,886 [4,279] km², using dBBMM and KDE, respectively) were 3.7–9.4 times larger than that of females (135 [86] km² and 411 [738] km², respectively). We found that greater chum salmon (*Oncorhynchus keta*) consumption was associated with larger annual home ranges for both sexes. In contrast, coastal brown bear populations that consume high levels of salmon often have small annual home ranges. We suggest that the relatively long distance (up to 100 km) between salmon streams and another key resource, denning habitat, is a reason for the positive association between salmon consumption and annual home range size. Although age was not in our top model for annual home range size, younger bears tended to have larger annual home ranges. We documented the fact that individuals of both sexes had the largest annual home ranges of any we could find for brown bears worldwide, using a traditional measure of space use (KDE). However, very large annual home ranges were associated with nonlocalized movements and the alternative method (dBBMM) to delineate these ranges provided more realistic range estimates. We discuss options and limitations of estimating space use and recommend caution when comparing space use between studies. With large-scale industrial infrastructure approved for development in this previously undeveloped region, the size and drivers of bear annual home ranges have numerous management implications. Brown bears with large annual home ranges in northcentral Alaska, where primary productivity is relatively low and denning habitat often far from salmon-bearing streams, are likely to move outside conservation units and encounter more risks as they interact with human infrastructure.

Key words: age, Alaska, body size, diet, dynamic Brownian Bridge Movement Model, Gates of the Arctic, grizzly bear, Kernel Utilization Distribution, *Ursus arctos*

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The area an individual animal utilizes to acquire requisite resources is known as its home range (Burt 1943)

and represents the physical manifestation of the realized niche of the individual (Hutchinson 1957). Factors known to influence home range size include body size, sex of the individual, presence of offspring, population density, habitat productivity–forage availability, spatio-temporal

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variation of resources, climate, predation risk, and disturbance (Seton 1909; McNab 1963; Lindstedt et al. 1986; McLoughlin et al. 1999, 2000; McLoughlin and Ferguson 2000; Dahle and Swenson 2003; Martin et al. 2010; Edwards et al. 2013; Mangipane et al. 2018).

Larger bodied species tend have larger home ranges because they have greater bioenergetic demands (McNab 1963, Lindstedt et al. 1986, McLoughlin and Ferguson 2000). Similarly, in sexually dimorphic species, the larger sex tends to have larger home ranges, which also may be related to bioenergetic demands (Harestad and Bunnell 1979). Larger individual sizes may increase competitive advantage for food, mates, and/or improve reproductive success (Kovach and Powell 2003; Isaac 2005; Hilderbrand et al. 2019a,b). In addition to smaller body sizes of females, lesser mobility of dependent young and changes to space use to reduce exposure risk of dependent young may also contribute to smaller home ranges (Lindzey and Meslow 1977, Hrdy 1979, Dahle and Swenson 2003, Libal et al. 2011). Although these factors are associated with smaller home ranges for females, the greater nutritional demand associated with lactation should drive the need for more food resources (Oftedal 2000) and thus potentially larger home ranges.

Habitats with greater primary productivity and resource availability can facilitate individuals meeting their energetic demands and, thus, reduce the size of their home ranges (McNab 1963). For some mammals, home range size has been correlated with an individual's age, with older animals tending to have larger home ranges. This correlation has been attributed to larger, mature animals needing more space to acquire nutrients and mates (Cederlund and Sand 1994). However, mature animals can dominate the most productive patches of habitat and/or cause younger animals to disperse, which would allow for smaller home ranges in dominant, older individuals and increase the estimated home range size of younger ones (Larter and Gates 1994, McLoughlin et al. 2000, Zedrosser et al. 2007). There may be learning and memory effects as well that result in smaller ranges (Van Moorter et al. 2009). Thus, we expect that in low-productivity habitats, older individuals would have larger home ranges (because of their larger size), whereas in high-productivity habitats, older individuals would have smaller home ranges (because of their dominant status).

Conceptually, a home range encompasses the total space use of an animal and its cognitive map of this space, including its perception (e.g., sight and smell) of the environment beyond the physical space it occupies (Powell 2000). Estimation of "home ranges" presents nu-

merous challenges and limitations and requires specifying the temporal extent being analyzed and choosing an appropriate estimation method (Laver and Kelly 2008, Fieberg and Börger 2012, Powell and Mitchell 2012). Here, we adopt the term "annual home range" as the space used by an animal over the course of their active season in a single year. We posit that the annual home range can be viewed as a sample unit for an individual's total, multiannual home range, and by considering multiple annual home ranges, we may approximate the conceptual total home range (such as when an asymptote in size is reached; also see Edwards et al. 2009). Animal behavior can also affect estimations of range use (Rooney et al. 1998, Noonan et al. 2019). For example, localized and nonlocalized (such as traveling to a distant resource) movement patterns may result in different patterns of space use (e.g., shape and overlap) and it is important to assess how a particular space-use estimator responds to observed movement patterns.

Brown bears (*Ursus arctos*) are a widely distributed, large omnivore. The annual home ranges of males have consistently been reported to be larger than those of females (e.g., Clarkson and Liepins 1989, Bjärvall et al. 1990, McLoughlin et al. 1999, Edwards et al. 2009). Similar to other species, this is thought to be driven by the larger body size of males and their ranging activities associated with searching for mates. In general, home range sizes of female brown bears with cubs have been found to be smaller than those of lone females; however, high variability results in differences that are often not statistically significant (Dahle and Swenson 2003, Edwards et al. 2013, Graham and Stenhouse 2014). Female brown bears with dependent young (cubs) are known to avoid male bears, which can result in the use of lower quality habitats and poorer diets (Ben-David et al. 2004, Steyaert et al. 2013).

Brown bears in environments with low productivity and resource availability, such as the Arctic, tend to have larger home ranges, which is likely due to the need to search further to acquire resources (Swenson et al. 1998, McLoughlin et al. 1999, Ferguson and McLoughlin 2000, Edwards et al. 2009). In contrast, in environments with greater productivity and resource availability, such as coastal areas with abundant salmon (*Oncorhynchus* spp.) runs, brown bears often have very small annual home ranges (Berns et al. 1980, McLoughlin and Ferguson 2000, McLoughlin et al. 2000).

Interestingly, Edwards et al. (2011) did not find a significant correlation between annual home range size and the diet of brown bears. Relatedly, the amount of meat in brown bear diets may not always translate to improved

body condition (Mangipane et al. 2020). Brown bears are ecologically plastic at the individual level and populations can have a diverse suite of foraging strategies (i.e., different home range sizes, habitat selection, diets), which can result in conspecifics that utilize different strategies reaching the same level of body condition (Hilderbrand et al. 2018a,b; Mangipane et al. 2020). A notable exception is coastal brown bears, which can readily access abundant salmon runs and typically have larger body sizes than do interior bears (McLoughlin and Ferguson 2000, McLoughlin et al. 2000, Cameron et al. 2020).

The effects of age on brown bear space use are relatively understudied. Although studies have shown that subadults have larger annual home ranges than adults, these differences are often not significant (e.g., Graham and Stenhouse, 2014). Dahle et al. (2006) showed that age was not related to home range size, but that study was limited to subadults. We are not aware of a study that has robustly analyzed for an effect of age on annual home range sizes while controlling for body size of individual brown bears.

Our objectives were to better understand the factors influencing the annual home range sizes of a population of brown bears in northcentral Alaska. This mountainous region lies entirely within the Arctic and has relatively low primary productivity, reduced resource availability, and extreme seasonality. However, there are spatio-temporally limited and heterogeneous areas of high-quality habitat (i.e., salmon streams). We predicted that larger bears would have larger annual home ranges because of their greater bioenergetic needs and mate-searching behavior. We predicted that male annual home ranges would be larger than those of females, supporting numerous studies documenting this trend (e.g., Swenson et al. 1998, McLoughlin et al. 1999, Edwards et al. 2009). Based on other studies, we predicted that large variation among individuals would mask differences in annual home range sizes between females with and without cubs. However, we predicted that individual females would have smaller annual home ranges when they had cubs-of-the-year (COY) than when they did not. Given the low, yet highly variable, productivity of the study area, we predicted a great difference in annual home range sizes between the sexes. We also predicted that, similar to coastal areas, bears with an abundance of salmon in their diet would have smaller annual home ranges. Lastly, within a given sex, we predicted that larger, older bears would have larger annual home ranges. To address our objectives, we applied 2 different statistical methodologies to delineate annual home ranges. We also discuss limitations of home range estimators, especially

when attempting to compare results between study areas and for certain behavioral types.

Study area

Our study area focuses on the portions of Gates of the Arctic National Park and Preserve (Gates) south of the continental divide of the Brooks Range Mountains (Fig. 1) and is centered on a proposed 340-km-long industrial road (Wilson et al. 2014). All of Gates and almost the entire study area is above the Arctic Circle. The climate is continental, with long (~8 months) winters with temperatures that regularly drop below -40°C . Summers are short (~2 months) but temperatures can reach 30°C . Northern portions and higher elevations are dominated by alpine and arctic tundra communities. The rugged peaks of this section of the Brooks Range can be up to 2,600 m high. Further south, the topography is less rugged and boreal forest, muskegs, and large rivers and lakes dominate the landscape. In this region, brown bears feed upon green vegetation, berries, and mammals, such as Arctic ground squirrels (*Urocitellus parryi*) and moose (*Alces alces*); however, despite being hundreds of kilometers from the ocean, individual bears in this population also consume chum salmon (*O. keta*) from a limited number of streams that are relatively (up to 100 km) far away from the mountains (Mowat and Heard 2006, Mangipane et al. 2020, Sorum et al. 2020).

Methods

Adult brown bears were located and anesthetized using Telazol (Fort Dodge Laboratories, Fort Dodge, Iowa, USA) via helicopter darting operations during spring (27 Apr–23 Jun) from 2014 to 2017 (Hilderbrand et al. 2018a). Capture and handling procedures followed Animal Care and Use approved protocols (“AKR_GAAR_Gustine_GrizzlyBear_2014”). All bears were instrumented with Global Positioning System collars (Telonics TGW-4680H-3, Mesa, Arizona, USA), programmed to collect relocations every 1.5 hours. Data were initially obtained via satellite link, but the data were also stored in the unit (“on board”) and were downloaded when it was retrieved. Erroneous relocations (e.g., distance exceeded likely movement rates [$> 10\text{ km/hr}$]) were filtered. We used all remaining relocations from the active period (i.e., when bears were not in their dens, typically Apr–Oct). We captured and instrumented 28 female and 8 male brown bears that collected enough data to calculate ≥ 1 annual home range. Some bear-years were characterized by long periods of missing data, so we only

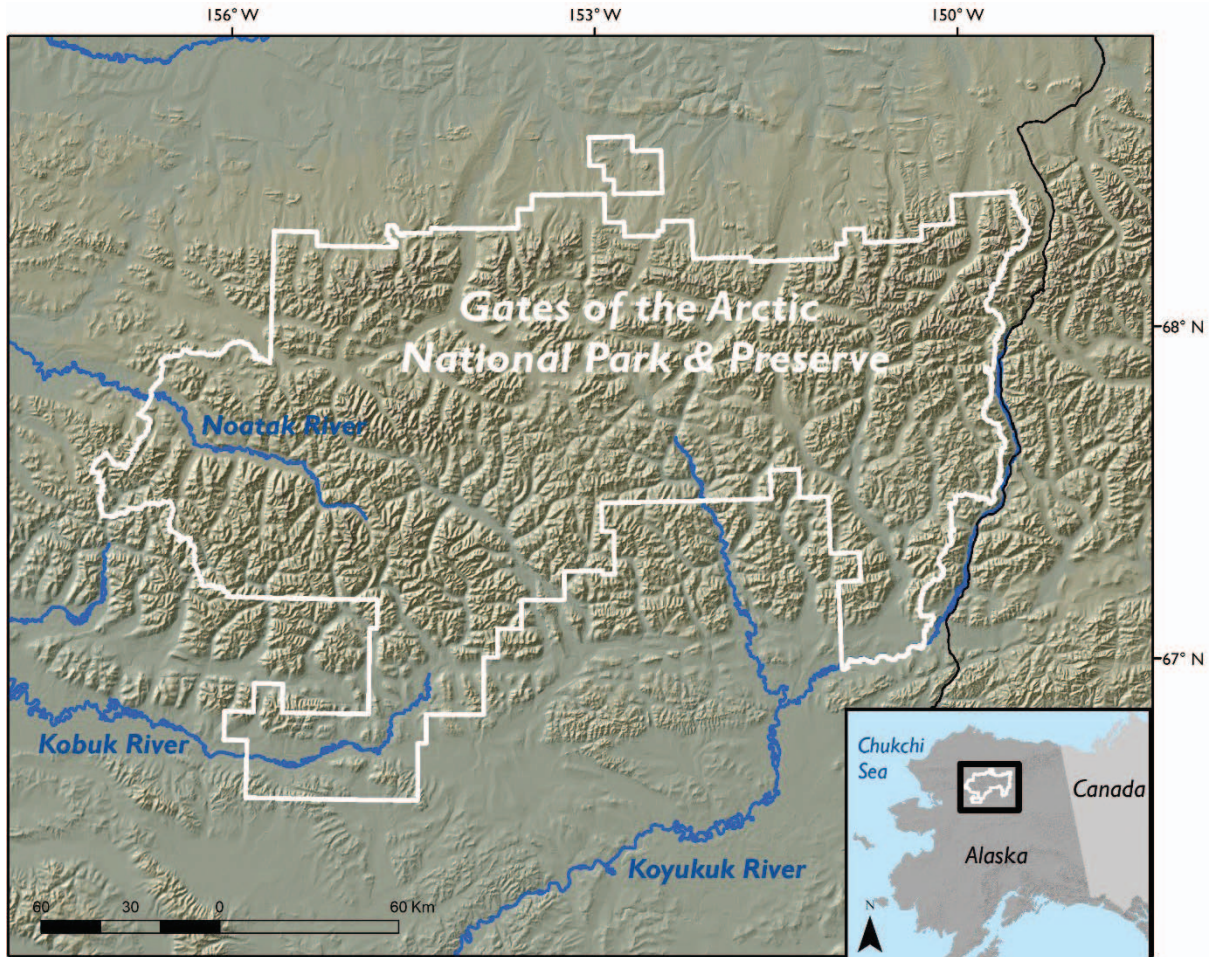


Fig. 1. Study area, central Brooks Range, Alaska, USA, for monitoring annual home range use of brown bears (*Ursus arctos*) from 2014 to 2017.

estimated annual home ranges for those with ≥ 800 relocations spanning ≥ 75 days to address this issue. We calculated annual home ranges for each individual, meaning that an individual collared in the spring of 2014 could provide annual home ranges for 2014, 2015, 2016, and 2017, if the collar remained active. Some collars lasted up to 3 years, so we were able to calculate 61 female and 14 male annual home ranges in total (Table 1). None of the bears appeared to disperse out of the study area.

We determined the sex of each bear, weighed it to the nearest 0.5 kg, and experienced observers estimated age from tooth wear (Hilderbrand *et al.* 2018a). With one exception, all bears were >5 years old at the time of capture. We also collected guard hair samples from between the front shoulders to estimate assimilated diet during

the previous autumn (Hobson *et al.* 2000). These samples were placed in individually labeled paper envelopes and stored in a -20°C freezer until analyzed. We utilized the percentage of salmon in the diet derived from these samples reported by Mangipane *et al.* (2020). For bears that had multiple years of diet estimates, we used the average of the estimates. This averaging, and the fact that estimates represent the diet of the individual from the year before sampling, meant that these diet estimates do not reflect the diet from the specific year of the annual home range estimates. We also recorded the presence, number, and age of offspring (COY or older cubs) accompanying females during capture and annually during subsequent aerial monitoring flights. To reduce the risk of abandonment or mortality, no offspring of any age were

Table 1. Average size and range (km²) of adult brown bear (*Ursus arctos*) annual home ranges in the central Brooks Range, Alaska, USA, 2014–2017. Annual home ranges were calculated as the 99% contour of a utilization distribution calculated from a dynamic Brownian Bridge Movement Model (dBBMM; Horne et al. 2007) or 95% contour of a kernel utilization distribution (KDE) applied to Global Positioning System locations during the active period.

Sex	<i>n</i>	dBBMM (SD)	Range dBBMM	KDE (SD)	Range KDE
Female	61	135 (86)	49–490	411 (738)	46–4,440
Male	14	504 (312)	175–1,206	3,886 (4,279)	322–12,518

captured. Some animals were caught multiple times during the study.

Minimum Convex Polygons (MCPs) and, more recently, Kernel Density Estimators (KDEs) have been the most widely used methods for estimating space use of large mammals. One goal of this study was to compare the annual home ranges of Brooks Range bears with estimates from other Arctic brown bear populations, so we determined the size of KDEs for our study animals. We calculated bear annual home ranges using the 95% contour of a kernel utilization distribution (UD). The KDEs were created with the ad hoc method to estimate the smoothing parameter, a raster resolution of 100 m, and with the package ‘adehabitatHR’ (Calenge 2006).

In the process of determining the size of annual home ranges for Brooks Range bears, we identified numerous individuals whose ranges appeared to be greatly overestimated, apparently as a result of their nonlocalized movement patterns. We were dissatisfied with KDEs to estimate the size of annual home ranges for these individuals, so we explored other methodologies. The dynamic Brownian Bridge Movement Model (dBBMM) is an extension of the Brownian Bridge movement model that incorporates time into estimating the UD of location data (Horne et al. 2007). The modification of the dBBMM is to incorporate behavioral changes into the UD estimation, offering flexibility across a range of behaviors. We estimated bear annual home ranges using the dBBMM with a raster resolution of 100 m, a window size of 31, and a margin of 11 (Kranstauber et al. 2012). Short time periods of missing data were problematic for a few individuals, so we adopted a conservative approach to estimate the UD by removing the motion variance associated with these gaps (effectively omitting a UD portion around the area with the missing data), ensuring a realistic UD (Kranstauber et al. 2020). We delineated an individual’s annual home range as the 99% contour of the fitted dBBMM UD using the package “move” (Kranstauber et al. 2020).

To investigate spatiotemporal patterns in annual home range sizes for bears with multiple years of data, we calculated the spatial overlap of all annual home ranges for

each bear. To do this, we calculated the area for which all years (either 2 or 3, depending on the individual) of annual home ranges overlapped for the individual, and calculated an overlap metric as the area of overlap divided by the largest of the annual home ranges (Breed et al. 2006). We performed a *t*-test to assess for differences in the amount of overlap between bears with 2 or 3 years of annual home ranges. For females with cub data, we analyzed for differences in annual home range sizes in 2 ways. First, we looked at females as a group, classified them as accompanied by cubs of any age or no cubs present, and performed a *t*-test to assess for significant ($P < 0.05$) differences in annual home range size. Then, we assessed how annual home range size of individual females changed with cub status by pairing annual home range estimates for the year they were observed with COY with the corresponding year when they either did not have any cubs or their cubs survived and were older, and we performed a paired *t*-test to test for differences.

To assess the effect of sex, age, body size (mass), and contribution of salmon to the diet on annual home range size, we used linear mixed-effect models with dBBMM estimates of annual home range size as the response variable. We incorporated a random intercept for bear ID to account for individuals with multiple seasons and log-transformed annual home range size to meet model assumptions of normality. We included a categorical covariate for salmon, in which ‘high’ denoted >30% salmon in the diet of the individual and ‘low’ was <30%, because no bear’s diet contained between 29% and 42% salmon. We built a candidate set of 14 models that assessed support for a combination of main effects and interactions and included a null model (Table S1, *Supplemental Material*). Correlations among continuous covariates were <0.5 and we performed model selection to identify a top-performing model (Burnham and Anderson 2002) using the Akaike Information Criterion corrected for small sample size (AIC_c; Hurvich and Tsai 1989). All analyses were performed in Program R version 3.6.2 (R Core Team 2019).

Table 2. Average size (km²) of adult brown bear (*Ursus arctos*) home ranges from across the Arctic. Sizes are for all males (M) and all females (F, with or without cubs). MCP is Minimum Convex Polygon and dBBMM is dynamic Brownian Bridge Model.

Location	M	F	Method	Reference
Northern Sweden	7,760		MCP	Swenson et al. 1998
Great Bear Lake, Canada	6,685	2,074	95% kernel	McLoughlin et al. 1999
Central Brooks Range, USA	3,886	411	95% kernel	This study
Anderson-Horton Rivers, Canada	3,433	1,182	MCP	Clarkson and Liepins 1989
Northern Sweden	1,825	593	100% MCP	Björvall et al. 1990
Northern Sweden	1,507	406	MCP	Swenson et al. 1998
Noatak River, USA	1,437	993	MCP	Ballard et al. 1993
Mackenzie River, Canada	1,215	680	95% kernel	Edwards et al. 2009
Tuktoyaktuk Peninsula, Canada	1,154	—	Weighted MCP	Nagy and Haroldson 1990
Northwest Alaska (NPR-A), USA	924	232	100% MCP	Reynolds 1978
Western Brooks Range, USA	872	225	MCP	Reynolds 1980 ^a
Eastern Brooks Range, USA	702	230	MCP	Reynolds 1976 ^a
Northern Yukon, Canada	645	210	MCP	Nagy et al. 1983 ^a
Central Brooks Range, USA	504	135	dBBMM	This study
Ivvavik National Park, Canada	447	149	MCP	MacHutchon 1996 ^a

^aCited in McLoughlin et al. (1999).

Results

Kernel Density Estimator annual home ranges

Male annual home ranges estimated using the KDE method were 9.4 times larger, on average, than female annual home ranges (Table 1). This disparity in annual home range sizes between sexes was the greatest we identified, globally, based on a literature search (see the 7.5 ratio in Björvall et al. 1990). The average annual home range size of 3 different male bears (12,518 km², 9,246 km², and 8,942 km²) and 1 female bear (4,440 km²) exceeded the greatest size we could identify anywhere for brown bears, based on the same literature search (8,264 km² and 2,904 km², respectively; see McLoughlin et al. 2000, Dahle and Swenson 2003, Graham and Stenhouse 2014). The annual home range sizes of both female and male brown bears under the age of 10 were greater than those 10 years and older (Table S2, *Supplemental Material*). Annual home range sizes of male bears were larger than most Arctic populations, whereas those of females were smaller (Table 2). Annual home ranges delineated with the KDE approach were very large for several bears that exhibited nonlocalized movement in the active season (e.g., Fig. 2).

Dynamic Brownian Bridge Movement Model annual home ranges

Overall, the dBBMM annual home ranges were much smaller than KDE annual home ranges for bears that exhibited nonlocalized movements, but they were similar in size for the bears that exhibited localized movements and had smaller KDE annual home ranges (Fig. 2).

The KDE annual home ranges were, on average, 3 times larger for female bears than those calculated with the dBBMM and >7 times larger for male bears (Table 1). Male dBBMM annual home ranges were >3 times larger, on average, than female ranges and exhibited greater variability (Table 1). The average coefficient of variation for individuals with multiple ranges was 0.22 (i.e., on average, the standard deviation [SD] was 22% of the mean range size). Average overlap of sequential annual home ranges was 44% (SD = 14%, range = 15–71%), and there was no significant difference in overlap metrics for bears with 2 or 3 years of data (2-sample $t[23.86] = 0.47$, $P = 0.64$). Annual home ranges of females with cubs (of any age) were not significantly different from those that did not have a cub (2-sample $t[43.60] = 1.37$, $P = 0.18$). However, individual females had a significantly smaller annual home range when they had COY than when they either did not have any cubs or had older cubs (paired $t[6] = -2.60$, $P = 0.04$). On average, annual home range size was reduced by 27.8% when an individual female had COY.

Modeling factors influencing dBBMM annual home range sizes

Our top model for factors influencing bear dBBMM annual home range size included main effects of sex and categorical (high or low) salmon in the individual diet. The next top performing model also included sex and an interaction with salmon in the diet and was separated by more than 2 AIC_c (Table 3). As such, we interpreted our results using only the top model. Overall, males had larger

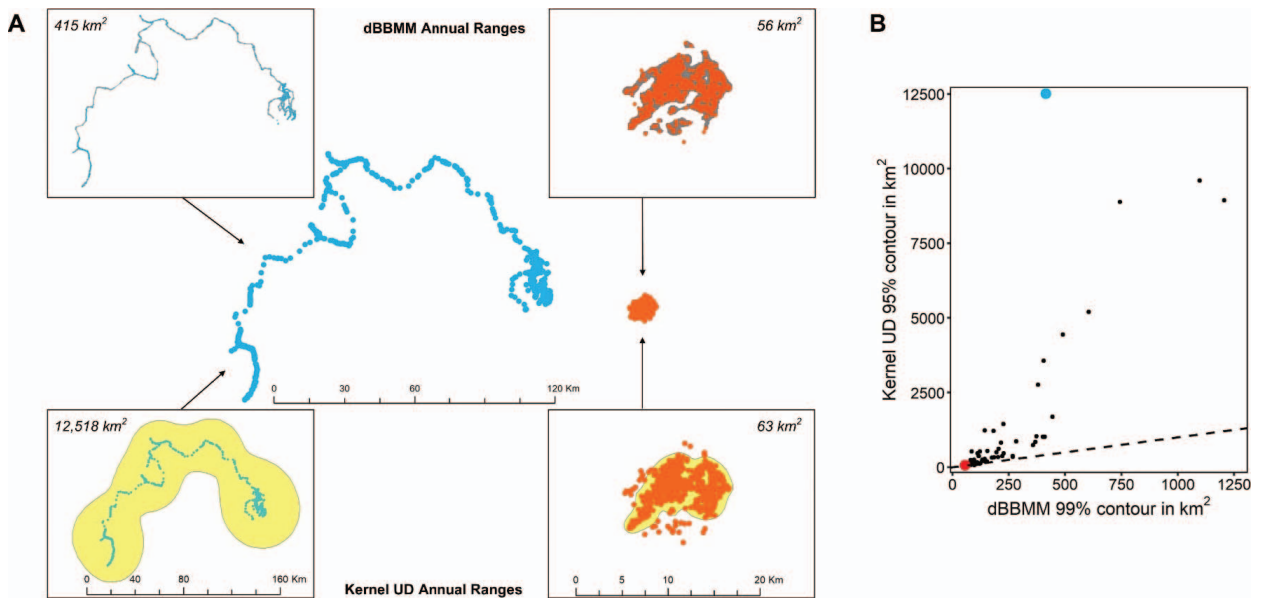


Fig. 2. A visual (Panel A) and quantitative (Panel B) comparison of the differences in annual home range size depending on methodology for brown bears (*Ursus arctos*) in and around Gates of the Arctic National Park and Preserve, Alaska, USA, 2014–2017. Panel A displays the Global Positioning System points (center) from 2 bears, one exhibiting nonlocalized (blue) and the other localized movement (red). Upper inset maps illustrate the annual home range (gray polygons) for the 2 bears using the 99% contour of a dynamic Brownian Bridge Movement Model (dBBMM), and the lower inset maps illustrate the ranges using the 95% contour of a kernel utilization distribution (Kernel UD; yellow polygons). Panel B contrasts the size of individual annual home ranges created by the 99% contour of a dBBMM (x-axis) and the 95% contour of a KDE (y-axis) for all bears, with the 2 bears in panel A corresponding to the same color scheme. The dashed line is the 1:1 line.

annual home ranges ($\beta_{\text{male}} = 1.5$; SE = 0.2; log-space) than did females (Intercept = 4.6; SE = 0.1; log-space), and bears that had high proportions of salmon in their diet, regardless of sex, had larger ranges than those that did not ($\beta_{\text{Salmon-High}} = 0.6$; SE = 0.2; log-space). This meant that both males and females that consumed salmon

had annual home ranges that were 75% larger than those that did not, respective to the same sex, and males that consumed salmon had the largest annual home ranges we detected (Fig. 3). Although mass and age were not in our top model, models with either covariate generally outperformed the null model (Table S1).

Table 3. Top 5 performing candidate models of annual home range size for brown bears (*Ursus arctos*) in and around Gates of the Arctic National Park and Preserve, Alaska, USA, 2014–2017. The response variable was log-transformed annual home range size (km^2), individual was included as a random intercept term, and “ \times ” indicates an interaction between 2 covariates. “Salmon H/L” indicates whether an individual had a diet of >30% salmon (high) or less (low).

Model	K	AIC _c	ΔAIC_c	AIC _c weight
~ Sex + Salmon H/L	5	70.3	—	0.7
~ Sex \times Salmon H/L	6	72.7	2.4	0.2
~ Sex + Mass	5	77.8	7.4	0.0
~ Sex	4	79.6	9.3	0.0
~ Sex \times Mass	6	80.1	9.8	0.0

Discussion

Contrary to our first prediction, we did not find evidence that body size (mass) was the strongest predictor of annual home range size for brown bears in this mountainous, Arctic region. However, larger bears tend to consume more salmon (Hilderbrand et al. 1999), so salmon consumption could have acted as a proxy for age and mass and masked the effect in our analysis. Brown bears in this region are known to be able to achieve similar levels of body condition (body, fat, and lean masses) using different strategies and having vastly different diets (Hilderbrand et al. 2018a,b; Mangipane et al. 2020). Thus, it is possible that the bears were able to achieve relatively similar physiological results with differing sizes of

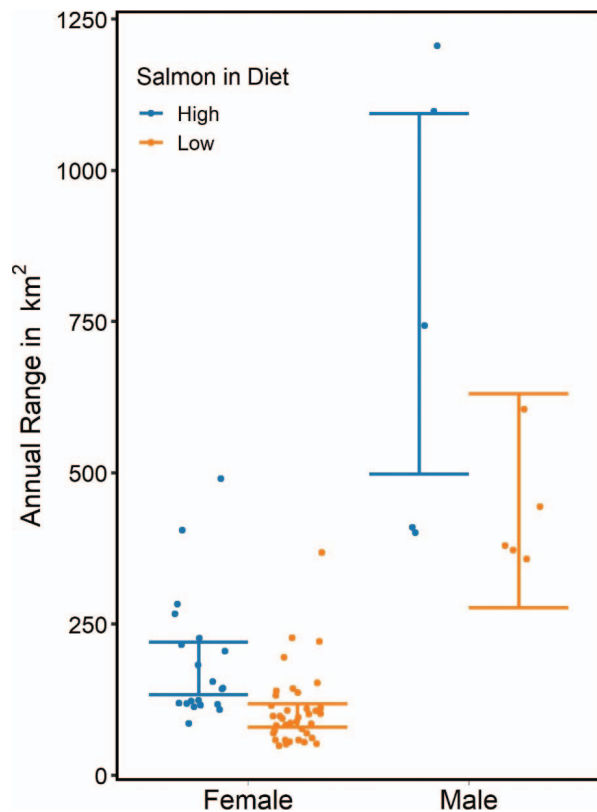


Fig. 3. Plotted top model of most important factors influencing annual home ranges (km^2) of brown bears (*Ursus arctos*) in and around Gates of the Arctic National Park and Preserve, Alaska, USA, 2014–2017. Top model included an additive effect of sex and category of salmon (*Oncorhynchus* spp.) in the diet of individual bears and estimated parameters are plotted as 95% confidence intervals. High is $>30\%$ and Low is $<30\%$. Raw data plotted as points. Bears that did not have data for all the covariates (e.g., missing body mass) were excluded from the modeling and are not presented in this figure.

home ranges by utilizing a variety of foraging strategies (Rogers 2021).

Although we did not find body size (mass) to be closely correlated with annual home range size, the sex of the individual was correlated. We expected annual home ranges of brown bear males to be larger than those of females, and we found that those of males were 3.7–9.4 times larger than those of females (depending on methodology). Our prediction that the annual home ranges of females with cubs and those without cubs would not be significantly different was supported, similar to other research (Edwards et al. 2013, Graham and Stenhouse 2014). We suggest that high individual variation tends to mask differ-

ences in annual home range size between females with and without cubs. Although mothers are accompanied by cubs for multiple years during development, cub mobility is most limited and vulnerability greatest in the first year of life (Lindzey and Meslow 1977, Dahle and Swenson 2003). Females with cubs may also restrict their space use to reduce their exposure to infanticide by breeding males (Lindzey and Meslow 1977, Hrdy 1979, Dahle and Swenson 2003, Libal et al. 2011). By comparing the size of annual home ranges of individual females when they had COY and when they did not (i.e., no cubs or older cubs), we found that the presence of COY significantly reduced annual home range size of the female (by 27.8% on average). We believe that the combination of reduced mobility of COY and an effort to reduce the risk of infanticide are drivers of smaller annual home ranges of females with COY.

Although we predicted that there would be a large disparity between the sizes of male and female annual home ranges, we did not expect to find some of the greatest disparities documented anywhere for this species. One factor that may influence this disparity is the low population density of our study area (Schmidt et al. 2021). Males may have to range further to acquire mating opportunities, which enlarges their home ranges. The spatial distribution of food resources may also contribute to the sex disparity in home range size. Within an otherwise low-productivity Arctic environment, there are spatiotemporally limited patches of high-quality habitat (i.e., salmon streams). Males are (>1.5 times) larger than females and rely upon salmon intake more than females do in this region (McDonough and Christ 2012; Hilderbrand et al. 2018b, 2019b; Mangipane et al. 2020). Salmon intake is known to affect the growth and productivity of bears (Hilderbrand et al. 1999) and, our results indicate, also their movements and annual home range sizes.

We predicted that bears with an abundance of salmon in their diet would have smaller annual home ranges. A superabundance of resources, such as salmon concentrated in spawning streams, can allow for small annual and home range sizes (McNab 1963, McLoughlin et al. 2000). However, our results revealed the opposite trend; bears that consumed higher levels of salmon had larger annual home ranges. We believe this relationship stems, in part, from the spatial location of another critical, yet heretofore largely unrecognized, resource that influences bear home range sizes: spatially distant denning habitat. In our study area, a mountainous, interior, Arctic-environment, denning habitat tended to be far from the streams where bears fished for salmon (Sorum et al. 2019). Thus, bears had to travel far from their dens to fish for salmon,

enlarging their annual home ranges. The exception was one male that denned near a salmon stream, and consequently had both high salmon intake and a relatively small annual home range. We suggest that other researchers investigating bear home range sizes also consider denning habitat and other critical resources when home range–resource relationships defy their expectations (or even when they do not).

We also predicted that typically larger older bears, within a given sex, would have larger annual home ranges. Although annual home ranges for both male and female bears <10 years old tended to be larger than those of older bears, the differences were not significant. We posit that the insignificantly larger sizes of the annual home ranges of younger bears may be related to ranging activities. In other words, less experienced, younger bears may make longer forays to establish their home range and acquire the skills and knowledge they need to survive. Age, and the knowledge and experience that comes with it, may help bears become more efficient foragers and thus reduce the size of their annual home ranges.

The annual home ranges delineated with the KDE method for many Brooks Range bears were exceptionally large. Although this was, in part, an artifact of the statistical methodology and the movement type of the individual, it does highlight the impressive displacement these bears displayed in the active season. As noted above, these large annual home ranges could be due to low habitat productivity and/or the distribution of specific resources (i.e., long distance (up to 100 km) between salmon streams and denning habitat). Another contributing factor may be the relative lack of physical boundaries. Most other study areas with published results have natural (coastlines) or manmade (roads, agriculture, development) boundaries that directly (i.e., act as a physical barrier) or indirectly (i.e., bears modify their behavior to avoid areas) restrict movement (Berns et al. 1980, Martin et al. 2010). The few studies of bear space use in locations away from coasts and with limited human development (e.g., low productivity, northern, interior habitats) also estimated very large annual home ranges (Swenson et al. 1998, McLoughlin et al. 1999).

Our study highlights some important caveats about the concept of home ranges, how they are estimated, and pitfalls of attempting to make comparisons among disparate studies. Our work reinforces recommendations that researchers specify the time period of the estimated home range, such as annual home range for delineations of a single year (also see Edwards et al. 2009), to improve clarity and repeatability, and ensure these periods are biologically meaningful (Laver and Kelly 2008, Fieberg

and Börger 2012). In our study, subsequent annual home ranges of an individual showed only a moderate level of overlap, which highlights the limited inference only a single season offers. We suggest that, as the cumulative area of sequential annual home ranges begins to asymptote, it likely begins to approximate the conceptual total home range of an animal. Differences in methodology (e.g., MCP, KDE, dBBMM), methodological specifications (e.g., 95% or 99% contours, or smoothing parameters), amount of missing data, and/or sampling regime (e.g., 4- or 8-hr relocation intervals) can have substantial impacts on the estimates of total and annual home ranges (e.g., Joly 2005, Fieberg and Börger 2012). Given all of these potential differences in how home ranges are estimated, interstudy comparisons should be undertaken with caution and skepticism when methodology is not completely identical. Traditional space use estimators, such as MCPs and KDEs, tend to work well on movements that are localized. We assert that dBBMM estimates of annual home range use provided more realistic determinations of space use for animals across the range of observed movements (e.g., migration, dispersal, nomadic) and was therefore more flexible in the broad application to our population. This was especially apparent for animals that returned to a location (like a den) after long movements (i.e., they made a loop). However, with ever-increasing technological advances, nearly continuous tracking of individual animals is foreseeable. Ultimately, this would collapse annual home ranges down to the footprint of the animal along its movement track. We do not believe this endpoint fully captures the intent of the home range concept either because it would likely exclude the cognitive map an animal builds of its home range (Powell 2000). We urge increased communication and collaboration among researchers so that identical methodologies are employed, which will allow for direct comparisons of space use by brown bears, or other species, among study areas. This is something that has not been widely done but could yield important insights into a species' ecology.

The large annual home ranges of brown bears in the central Brooks Range have important management implications. Although much of the Brooks Range is covered by land conservation units and contains extensive denning habitat (Sorum et al. 2019), the annual home ranges of many bears extend outside protected areas. This is especially true for the relatively large percentage of both male and female bears that utilize salmon as an important component of their diet. Thus, managers should not assume that the sheer size of large, protected areas ensures a wildlife conservation outcome. Empirical movement data from wildlife often demonstrate that even the largest

protected areas may not encompass all facets of important habitat and critical resources required to maintain healthy wildlife populations, especially for migratory species or species with large home ranges. Managers should consider the relative risks (e.g., vehicle collisions, harvest) and rewards (e.g., obtaining nutrient-rich resources like salmon) of animal movements, as well as the distances and routes traveled to achieve individual and population needs. Harvest is relatively low within Alaska conservation units (where it is generally restricted to a limited number of rural residents and by difficult access), but greater access allows for more hunters outside of them (Schmidt et al. 2021). Salmon streams, especially the larger ones, may facilitate greater harvest of bears as a result of aggregation during salmon spawning. Additionally, planning for the construction of a 340-km industrial road, which will run between denning habitat of Brooks Range bears and many of the salmon-bearing streams in this region, is underway (U.S. Bureau of Land Management 2020). Our findings highlight that, despite spending a large part of the active season within a conservation unit, bears in this region, especially those that rely on salmon in their diet, would interact with this road and the human activities concentrated along it. Placement of facilities, such as road construction and maintenance stations, material pits, and other infrastructure that facilitates high levels of human use should take into consideration these movements.

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Supplemental material

Table S1. Complete model set results for testing for influences of factors on annual home range size of brown bears (*Ursus arctos*) in Gates of the Arctic, Alaska, USA, 2014–2017. Response variable was log-transformed annual home range size (km²), individual was included as a random intercept term, and “x” indicates an interaction between 2 covariates.

Table S2. Brown bear (*Ursus arctos*) data, Gates of the Arctic National Park and Preserve, Alaska, USA, 2014–2017.