Surveys

Application of a Double-Observer Aerial Line-Transect Method to Estimate Brown Bear Population Density in Southwestern Alaska

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Abstract

Brown bear *Ursus arctos* population density was estimated for a 21,178-km^2 study area in southwest Alaska. Estimates were obtained using an aerial line-transect method that allows for peak detection to be both off the transect line and less than 100%. Data collection required five small aircraft with 2-person crews. Surveys were flown in 10-d windows to capture the period after den emergence but prior to full green-up. Surveys were flown in two consecutive years in order to detect sufficient bear groups to support the estimation. The study detected 197 bear groups (330 bears) in 969 aerial transects averaging 24.8 km long and with a strip width of 728 m. Estimated population density in the study area was 40.4 bears/1,000 km^2 (95% CI = 31.4–54.5); estimated density of independent bears was 27.3 bears/1,000 km^2 (95% CI = 21.4–34.4). Assuming similar estimate precision, repeating the survey could detect population changes of approximately 38% or larger with a power of 80%. We find the method suitable for regions of relatively high bear population densities or detection rates.

Keywords: *Ursus arctos*; population estimate; double count; contour transects; distance estimation; gamma detection function; aerial line transects

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Introduction

The brown bear *Ursus arctos* is the largest member of the order Carnivora in southwest Alaska. It occupies the uppermost position in a complex food chain, plays a primary role in the distribution of nutrients from aquatic systems to terrestrial systems (Helfield 2001), and is a continuing source of human interest, both positive and negative. It occurs in a variety of habitats (e.g., grasslands, tundra, forests) ranging from mountain tops to coastal beaches.

Efforts to estimate Alaskan brown bear populations have been evolving since the 1930s (Dufresne 1967). Brown bear populations are often difficult to monitor due to low population density, low detectability, and winter inactivity (Kansas 2002). Estimation methods have included relative abundance indices based on incidental observations (Elgmork 1991) or track counts (Valdmann et al. 2001), mark–recapture using visual observation (Swenson et al. 1994; Miller et al. 1997) or genetic signature (Boulanger et al. 2002; Bellemain et al. 2005), total counts with sightability corrections (Barnes and Smith 1998), and distance estimation methods (Quang and Becker 1997).

Brown bear population density was first estimated in this study area as part of a statewide population assessment (Miller 1993) that classified Alaskan brown bear populations into three density classes: low density ($<$ 40 bears/1,000 km^2), medium density (40–175 bears/1,000 km^2), and high density ($>$175 bears/1,000 km^2). Probable brown bear population density was mapped statewide by extrapolating from 17 study areas. The present study area was included in the low-density category. More recently, a demographic study in the Kuskokwim Mountain portion of the Togiak and Yukon Delta National

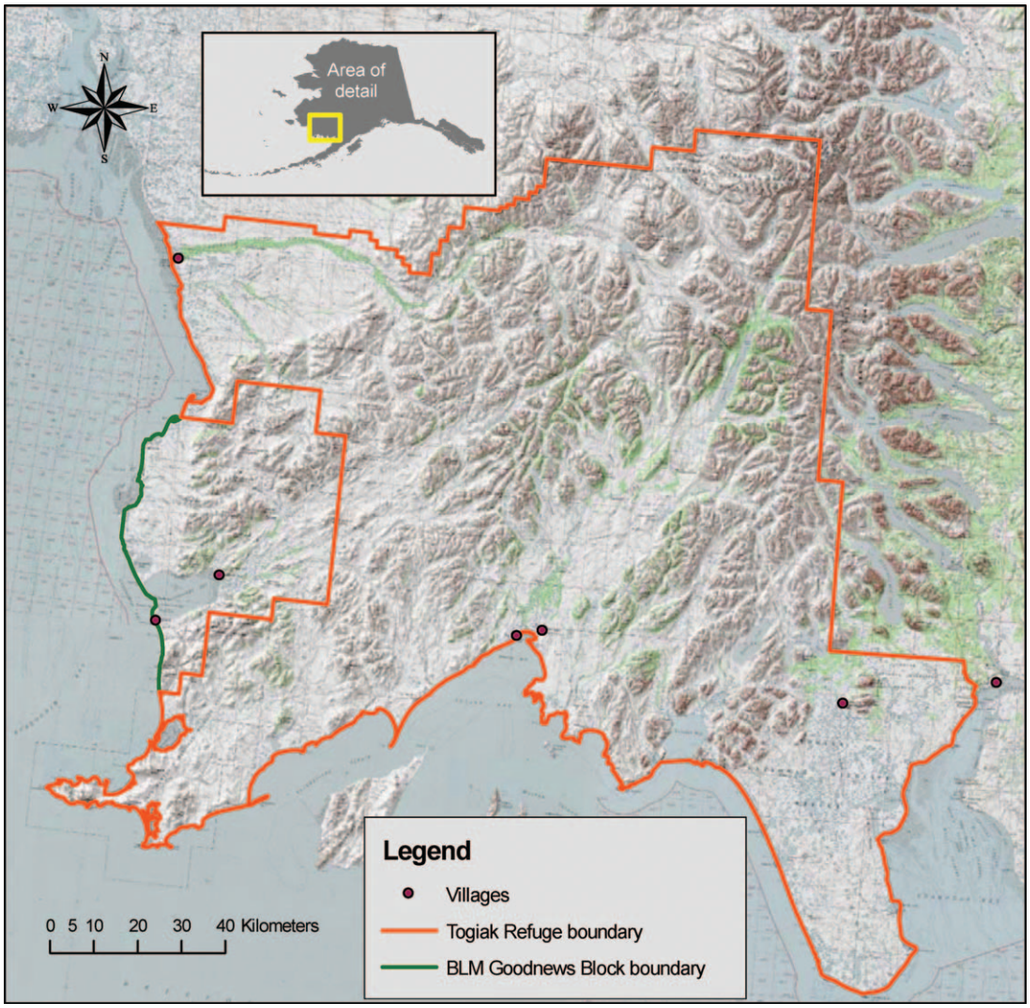

Figure 1. Study area.

Wildlife Refuges and Wood-Tikchik State Park encountered 52 known independent bears (defined as bears 3 y or older no longer dependent upon their mothers). This count provided the basis for a minimum brown bear population size for the area equating to a density of 18.2 independent bears/1,000 km^2 (Van Daele et al. 2001). However, the researchers suspected that actual density was nearly twice that size (Van Daele et al. 2001).

In recent years, concerns have been regularly voiced during local village meetings, state Fish and Game Advisory Committee Meetings, and Federal Subsistence Regional Advisory Council meetings, that brown bear populations are increasing, and this increase has adversely affected wildlife populations targeted by subsistence hunters. The lack of quantitative information on bear abundance has prevented resource managers from adequately addressing these concerns.

This project was initiated to: 1) estimate the number of brown bears, and its associated uncertainty, throughout Togiak National Wildlife Refuge and the Bureau of Land Management (BLM) Goodnews Block; 2) report time and effort requirements to conduct this study and discuss feasibility as a monitoring method; and 3) estimate demographic parameters of brown bears throughout Togiak Refuge and the BLM Goodnews Block.

Study Area

The study area consists of Togiak National Wildlife Refuge, the BLM Goodnews Block (Bureau of Land Management lands in the vicinity of Goodnews Bay), and various private and native corporation lands enclosed within the outer boundary of the two federal land units (Figure 1). The study area comprises approximately 2.12 million ha. Land forms in the study area are dominated by the Ahklun Mountains, which occupy approximately 80% of the area. The remainder consists of low-elevation graminoid and lichen tundra areas forming the Nushagak and Kanektok Lowlands at the southeast and northwest edges of the study area. The area includes approximately 1,120 km of coastline at the confluence of the Bristol and Kuskokwim Bays of the Bering Sea. It includes whole or portions of 35 major rivers, 25 major lakes, and extensive smaller water resources (USFWS 1990).

The study area climate is subarctic maritime near the coast, transitioning to subarctic continental toward the interior. From 1971 to 2000, the mean monthly maximum and minimum temperature averaged −6.3°C and −11.3°C in February, the coldest month, and 11.9°C and 8.4°C in August, the warmest month (data for Cape Newenham Air Force Site in the

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southwest corner of the study area; NOAA 2008). Precipitation averaged 90.1 cm annually and total snowfall averaged 197.8 cm annually during the period 1953–1984.

The marine and aquatic environments are highly productive, especially for the five species of Pacific salmon, over 1,000,000 of which return annually to spawn in study area waters (USFWS 1990). Brown bear reproductive success, population density, and body size have all been correlated to the availability of high-quality food sources such as salmon (Hilderbrand et al. 1999).

The study area is relatively undeveloped, with most human development restricted to seven villages (Figure 1) with a total human population of approximately 5,000. There is no network of roads among villages. Villages are located at the mouths of the majority of the largest rivers. During the time of the study, there was virtually no human activity on the study area, save that associated with villages and aircraft flights.

Most brown bears in the study area emerge from dens in mid-May (Collins et al. 2005). However, some remain in their dens until mid-June. Of 231 locations of radiocollared female brown bears studied 1994 through 2003 in a study area that included the north-central portion of the current study area, 22 (9.5%) were recorded as still in their dens between 25 May and 6 June. Further, 17 (7.4%) were known or estimated to emerge between 1–13 June (Togiak National Wildlife Refuge, unpublished data). During the year that this study was initiated, 1 of 21 radiocollared bears was in its den on 19 May (Togiak National Wildlife Refuge unpublished data); it had emerged when located 1 mo later.

Methods

Overview

The study used the double-observer aerial line-transect method (Quang and Becker 1999; Becker and Quang 2009). The method combines distance sampling and double-observer techniques to allow maximum probability of detection (''peak detection'') to occur off the transect centerline and be less than 100%. Survey effort is driven by the need for sufficient detections to estimate the detection function (Buckland et al. 2001). This method does not require assumptions about spatial distribution of bears (Buckland et al. 2001). Population closure is assumed, including if multiple years are required to attain a sufficient number of detections. Although this assumption cannot be perfectly met over years, there is evidence that population change is low. In a study of female brown bears in the vicinity of the current study area from 1993 to 2002, Kovach et al. (2006) estimated λ to range annually from 0.949 to 1.056. All study area bears are assumed to be available for detection (as opposed to being in dens and, thus, undetectable).

Survey design

Surveys were performed from tandem two-seat aircraft (Piper Supercub and Aviat Husky) capable of slow speed and high maneuverability. Transects, generally 25 km long, were surveyed 90 m above ground level at approximately 95–125 km/h. The pilot and backseat passenger both served as observers, but will henceforth be referred to as ''pilot'' and ''observer.'' Prior to the study, pilots and observers were briefed on the survey protocol and underwent a mock survey on the ground to gain familiarity with the data-recording protocol and use of the data-collection software on portable computers.

Transect selection. Transect midpoints were randomly selected throughout the study area at all elevations up to 1,067 m following Alaska Department of Fish and Game protocol (E. Becker, Alaska Department of Fish and Game, personal communication). In flat terrain, transects followed straight paths with a random angle at the midpoint in order to better fit into a partially mountainous landscape. In mountainous terrain, transects followed the contours of the land to maintain a constant elevation (Quang and Becker 1999). When a continuous 25-km transect was not possible at a given elevation (such as in the case of a lone mountain), the transect was paused when the mountain was circled, then resumed on the nearest unsurveyed mountain. In cases where there were no nearby areas of the appropriate elevation, transects were shorter than 25 km. In total, 1,200 transects were randomly selected from across the study area. Transects were randomly ordered, then the first 100 transects were surveyed, then the next 100, etc., in order to avoid confounding of location and survey date. Both individuals observed to the same side of the aircraft when flying a transect. In flat terrain, the side was randomly chosen by flipping a coin; on contour transects, observations were made on the uphill side.

Survey timing. Surveys were timed to commence after brown bears emerged from their dens, based on den emergence information from Collins et al. (2005), and conclude prior to when full vegetation leaf-out reduced detectability. Continuing den emergence during the study would violate the assumption that all bears were available to be detected, resulting in density estimates that were biased low. Similarly, advancing leaf-out during the study would violate the assumption of a temporally constant detection probability and require further modeling to account for the heterogeneity.

Survey protocol. Location of flight path and transect attributes (start point, end point, deviations from the transect) were recorded by a portable computer interfaced with a Global Positioning System (GPS) using a custom application for ArcPad version 6.0 (ESRI 2002). The observer recorded covariates describing the bear group, surrounding area, and transect information (Table 1). Vegetation cover and snow cover were estimated in comparison to a reference card illustrating cover levels at 10% increments.

Additionally, at each bear group observation, an estimate was made of the furthest distance being actively searched at the time of the observation (referred to as the effective search distance, or ESD). Effective search distance recorded the instantaneous width of an observer's active search area. The covariate changed with both terrain and habitat; it was shorter on contour transects in high-gradient terrain due to visual blocking by the wings, and shorter in denser vegetation due to slower search rates; hence, there was a narrower search area for a fixed flight speed. An ESD was recorded for the person who detected the bear group; when both parties detected the group, an agreed-upon common ESD was recorded. Bear group and ESD locations were recorded via GPS by having the aircraft deviate from the transect and fly directly over the bear group (or the initial point of observation if the group had since moved) and the ESD point. Additional covariates continuously recorded while on a survey transect included time of day, speed, GPS location accuracy, and aircraft altitude.

In order to maintain independence of observations, pilot and observer did not inform one another of observations of each bear group until after the aircraft had passed the group. After passing, information was exchanged to determine who saw the bear group: pilot only, observer only, or both. A visual barrier was placed between pilot and observer to ensure independence of observations.

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Table 1. Covariates recorded at the observation of each bear group.

Covariate	Response
Transect ID	Unique number designating each transect
Search side	Right or left
Bear ID	Unique number assigned to each bear group
Number of bears	Total number of bears in group
Group type	One of the following:
	Male
	Female
	Breeding pair
	Subadult(s)
	Female with cub(s) of the year
	Female with yearling offspring
	Female with 2-y-old or greater offspring
Activity type	One of the following:
	Bedded
	Sitting
	Standing
	Feeding
	Walking
	Running
% Cover within 10 m	Estimated percentage of area within 10 m of bear group that would obscure bear group visibility
% Snow	Estimated percentage of area within 10 m of bear group covered with snow
Who observed?	One of the following:
	Pilot
	Observer
	Both
Repeatability	The estimated number of times out of 10 one would have seen the bear group under similar conditions

Data were initially processed following each daily survey, then collectively prior to analysis. Processing details are discussed in the *Supporting Information*, Text S1 (http://dx.doi.org/10.3996/062009-jfwm-006.S1). The minimum sample size to achieve estimates of adequate precision (defined as those with CV of $\sim$ 0.15) was estimated to be 150 bear groups (E. Becker, Alaska Department of Fish and Game, personal communication). The study was scheduled to continue a second year if necessary to achieve this goal.

Density estimation

The density estimate for the study region was obtained in two phases: (i) estimating a detection function, thus providing estimates of each bear group's probability of detection, then (ii) using the probabilities of detection and observed bear group sizes to estimate bear group density in the searched region (Becker and Quang 2009; Buckland et al. 2001). By sampling design, this also estimates bear density in the study area.

The uncertainty of the resulting density estimate is a function of two components. Foremost is the uncertainty in the fitted detection functions, predominantly driven by the total number of groups detected and the sources of systematic variation in the detection probability. The other component is variation in group size, which only becomes a factor in phase (ii) of the estimation.

Total area searched also only comes into play in phase (ii), estimating the bear density in the search region. In this context, interest is in the total area actively searched—if a particular transect is flown twice, its search area is counted twice. Thus transects overlapping in space but not time, or repeated observations of the same bear group at different times (on different transects), etc., do not invalidate the method or introduce bias. Bears moving within the study area do not bias estimates if their average speed is less than 33–50% of survey aircraft speed (Hilby 1986).

Fitting detection functions. Estimates of pilot and observer peak detection probabilities were obtained from the double-count data using maximum likelihood as described in Becker and Quang (2009). Detection functions were estimated by fitting a gamma distribution kernel to the observed detection distances (Becker and Quang 2009). For flexibility, the scale parameter was modeled as the product of two components: $b \cdot \lambda$, where b was a function of the shape parameter r (see below) and λ was a log-linear function of observed covariates (see below; Becker and Quang 2009). Thus, covariates could influence the "scale" of the detection function, stretching the function to the right or left, but not the overall shape.

Although ultimately combined, detection functions were initially fit separately for the pilot and observer to allow for differences in detection. Following Becker and Quang (2009), detection functions were modeled as

$$\mathrm{Pr}_{\mathrm{detect}}(y|h_j,r_j,\lambda_j) = \frac{h_j}{\Gamma(r_j)b_j}\left(\frac{y}{\lambda_j b_j}\right)^{r_j-1}\exp\left(\frac{-y}{\lambda_j b_j}\right) \qquad (1)$$

where y is the perpendicular distance from the transect to the

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Table 2. Summary of annual survey effort and detected bear groups.

	2003	2004	
Survey dates	**19–29 May**	**24 May–2 June**	**Total**
Transects surveyed	474	495	969
Average transect length (km; SD)	24.87	24.72	24.79 (1.46)
Total survey length (km)	11,789	12,237	24,026
Transects with detected bear groups	83	82	165
% Transects with detected bear groups (SD)	17.5% (2%)	16.6% (2%)	17.0% (2%)
Bear groups detected	99	98	197
Total bears detected	163	167	330
Average bears/group (SD)	1.65 (0.94)	1.74 (0.84)	1.70 (0.89)

detected object, j distinguishes between the detection parameters of pilot and observer functions, h is the maximum detection probability at the function's apex, r is the shape parameter, and λ is a nonlinear function of the covariates (below); the scale parameter is $b \cdot \lambda$, where

$$b = \frac{1}{\Gamma(r_j)}\left(\frac{r_j - 1}{e}\right)^{r_j - 1}; \quad (2)$$

e is the natural logarithmic base. Covariates were incorporated via a log-linear model:

$$\ln(\lambda_j) = \beta_{jo} + \beta_{j1}x_1 + \ldots + \beta_{jk}x_k \quad (3)$$

where the x_i are the covariates associated with the ith group detected by observer j (i.e., the pilot or the observer).

The suite of plausible detection functions, or models, was identified using a three-step process. Final density estimates were obtained from the best model as identified by model selection using Akaike's information criterion (AIC; Burnham and Anderson 2002).

Model selection step 1: covariate screening. Categorical covariates (Table 1) were reviewed, independent of detection distances, and categories combined, if possible, to reduce the total number of parameters. Temporal changes in den emergence, green-up, searcher experience, and searcher exhaustion could create nonlinear changes in detection across time. For example, while green-up increased with survey date, potentially decreasing detection of bears, searcher experience simultaneously increased, potentially increasing detection of bears. This was accounted for by including both quadratic and linear effects of survey date in modeling detection. Differences between years were accounted for by including interactions between study year and date.

Consideration was only given to models where (number of detected bear groups)/(number of covariate parameters) was ≥ 10 (van Belle 2002). For example, for fitting the pilot detection function, the relevant number of detected bear groups was the number detected by the pilot and both pilot and observer. All covariates associated with models whose AIC values were within 10 of the best fitting model's AIC, for either the pilot or observer model suites, were considered further.

Model selection step 2: independent fitting of pilot and observer models. All single covariate detection functions were fit separately for pilot and observer and their AIC values and weights calculated (Burnham and Anderson 2002). To limit the number of models, only covariates from the four models with the lowest AIC values from each analysis (pilot or observer) were used. These were combined with interactions between year and date to form models for further analysis. These were fit

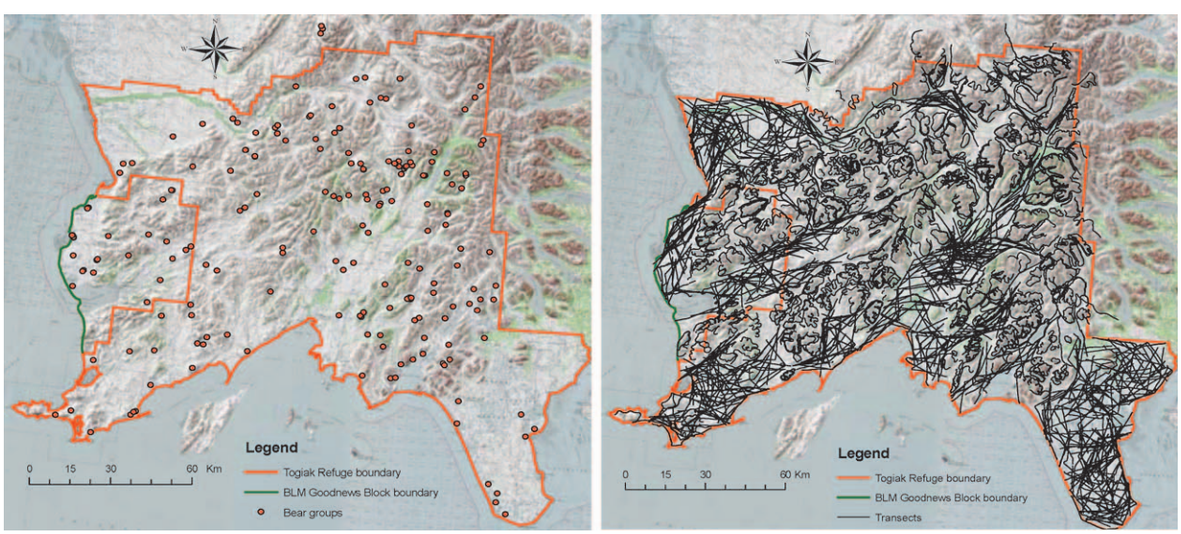

Figure 2. Location of bear groups observed (**left**) and transects surveyed (**right**) during spring 2003 and 2004.

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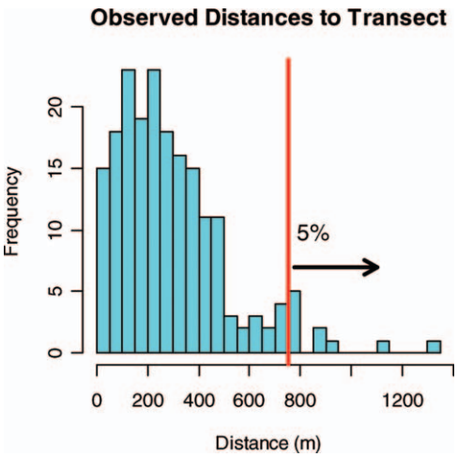

Figure 3. Observed detection distances and resulting strip-width estimate.

for pilot and observer separately and their AIC values and model weights calculated.

Observations can have different detection functions if covariate values differ. They can be transformed to a common distribution using the fitted model (if the model fits; Becker and Quang 2009). Model goodness-of-fit was assessed by using the Kolmogorov–Smirnof test to compare the transformed observations to the common distribution. The test null reference distribution was generated by Monte Carlo simulation to account for use of the fitted model parameters in the transformation (Tadikamalla 1990).

Model selection step 3: top combined model. The best pilot model and the best observer model were refit to the pooled data and combined into a single model.

Temporal trend in detection. At least four different causes could produce a within-year temporal trend in bear group detections: 1) increasing numbers of bears available for detection due to survey initiation prior to 100% den emergence, 2) increasing detection rate due to increasing observer skill, 3) decreasing detectability due to increasing vegetation green-up, and 4) decreasing detectability due to increasing observer exhaustion. Temporal trends in bear group detections were assessed by regressing each day's bear group encounter rate (number of bear groups detected/total length of transects surveyed) against the survey date using weighted regression (weights proportional to total length of transects surveyed per day). Each year was assessed separately.

Density estimation. Having identified the best combined detection-function model, the number of bears in the searched area was estimated as Σ(bear group size)/(probability group was detected), where probability of detection (by either pilot or observer or both) was calculated from the fitted detection functions (Becker and Quang 2009). Bear density was estimated by dividing the estimated number of bears by the total area searched. Each transect's search area was estimated as the area perpendicular to the transect out to the strip-width distance, less a blind strip of 22 m directly alongside the transect and, hence, underneath the airplane (Becker and Quang 2009). The strip width was defined as the 95th percentile of the observed detection distances (Buckland et al. 2001). For curvilinear transects, area that was lost or gained due to transect curvature was calculated using geographic information systems (GIS) macros written in ArcInfo version 9.0 (ESRI 1999). Total search area was estimated as the sum of the transect search areas. Note that for many contour transects, topographic relief limited the searchable width to less than the strip width identified from these calculations. Thus, overall searched area was overestimated and true density underestimated by an unknown amount. However, assuming later surveys sample similar numbers of contour and flat transects, the bias in total search area will remain relatively constant, allowing for accurate assessments of change. The density estimation process was repeated for sows with offspring categories to estimate the population density of independent bears.

Standard errors and confidence intervals. Nonparametric bootstrap resampling (n = 2,000) of transects was used to estimate standard errors and 95% confidence intervals for all major model parameters and estimates. Percentile and bias-corrected adjusted confidence intervals were calculated (Lunneborg 2000).

Change detection. The feasibility of using this method to monitor meaningful population change in a reasonable period of time was assessed as follows. The first step was to determine the minimum change detectable with 80% power between two sampling events. This was approximated using a two-sided two-sample t-test and assuming equal sample sizes and sampling variances for each period:

$$\mu_0 - \mu_t = \sqrt{2}\cdot(Z_{1-\alpha/2} + Z_{80\%})\cdot \mathrm{SE} \quad (4)$$

where Z_x is the xth quantile of the standard normal distribution and SE is the assumed standard error of each abundance estimate (van Belle 2002). The next step was to convert the minimum detectable change, $\mu_0 - \mu_t$, into the associated finite rate of population change (λ), assuming the two surveys were taken t y apart:

$$N_t = N_0\lambda^t, \text{ so} \quad (5)$$

Table 3. Revision of covariates used for modeling the scale parameter of the detection function.

Covariate	Scale or original levels	Revised
Group activity	Bedded, sitting, feeding, standing, walking, running	Alternative 1: low (bedded, sitting), medium (feeding, standing), high (walking, running);
		Alternative 2: low (bedded, sitting, feeding, standing), high (walking, running)
Group size	1, 2, 3, 4	1, 2, 3+
Group type	Adult male, adult unknown gender, subadult, breeding pair, sow w/cub, sow w/yearling, sow w/2-y-olds	Adult male, sow w/young, other
Visual index combining snow and vegetation cover (Figure 4)		High (snow ≥ 30%, vegetation ≤ 20%), medium (all others), low (snow ≤ 10%, vegetation ≥ 40%)

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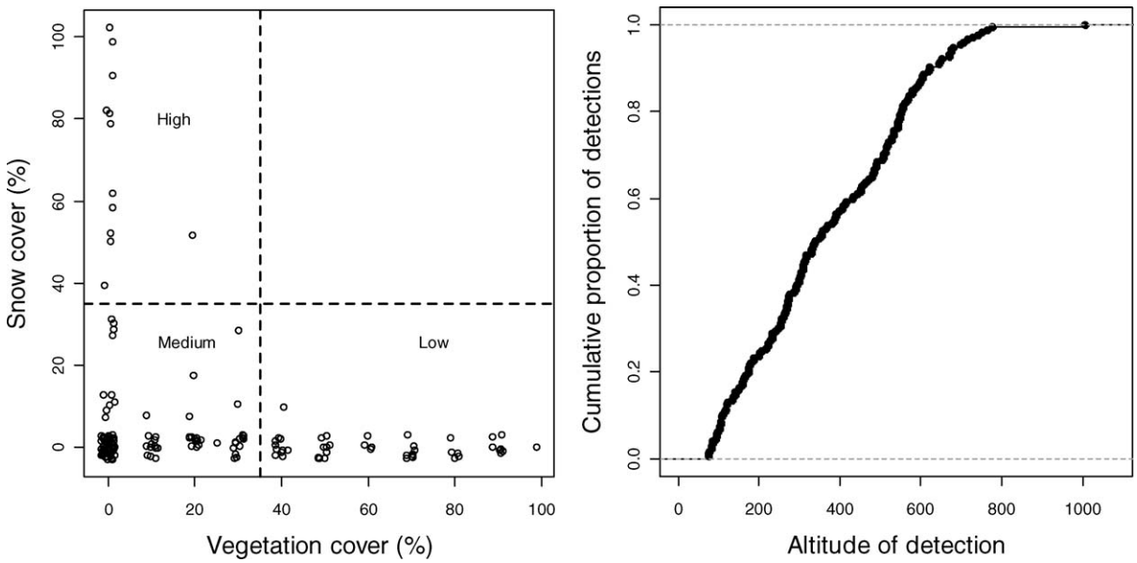

Figure 4. (Left) The ordinal vegetation and snow-cover covariates were combined into a three- level visual contrast index (labeled regions). **(Right)** The cumulative distribution of altitudes (= elevation + aircraft height) at which bear groups were detected (unadjusted for height of airplane above ground level).

$$\lambda = \left(N_t/N_0\right)^{1/t} \quad (6)$$

where $N_0 = \mu_0$, the abundance estimate from the initial survey, and $N_t = \mu_t$, the final abundance estimate (Skalski et al. 2005).

Software. Transect selection and estimation of detection distances and search areas were performed using GIS (ESRI 1996a, 1996b). All graphs and analyses were conducted in R (version 2.2.0; R Development Core Team 2005) with supplemental packages for numerical optimization (Geyer 2005) and bootstrapping (Canty and Ripley 2005). The analysis code is available upon request to the second author.

Sex and age composition

If detection probability was found to be independent of group type or size, then bear groups could be considered a random sample of the brown bear groups in the study area and simple summaries calculated of bear demographics, group sizes, and activities. However, there was no assessment of observer accuracy in classifying bears to age or gender. Thus, although all bear group classifications are reported as recorded by observers, demographic inferences are restricted to females with offspring because we assume the size difference between sows and their offspring resulted in low classification error rates.

Table 4. Change in AIC (ΔAIC) among the suite of single covariate models for the scale parameter, for Pilot and Observer data fit separately.

Covariate	Pilot ΔAIC	Observer ΔAIC
Intercept only	32.0	47.19
ln(ESD)[a]	0	0
Date	29.22	45.79
Year	30.48	47.63
Group activity (original)	32.86	43.88
Group activity (revised, alternative 2)	31.92	42.46
Group size	33.41	47.56
Group type	35.00	47.78
Visual index	34.28	47.70

[a] ln = natural logarithm. ESD = effective search distance.

Results

Study effort

The study was initiated in 2003, at which time 99 bear groups were detected. Because this was fewer than the desired sample size of 150, the study continued in 2004, resulting in a study total of 197 detected bear groups (Table 2; Figure 2). A total of 969 transects were surveyed, with survey effort fairly evenly distributed across years. Average survey speed was 118 km/h (range in average of individual transects: 47–181 km/h).

Detection-function estimation and selection

Strip width. Eliminating the largest 5% of the observed distances (Buckland et al. 2001) gave a strip-width estimate of 750 m (Figure 3). Only bear groups whose detection distances were less than this value were considered in the detection-function estimation process, though all detected bear groups were considered in the demographic summaries.

Covariate screening. Seven covariates were initially considered for use in fitting the scale function λ, addressing survey timing (Date, Year), habitat or terrain surrounding the detected bear group (Effective Search Distance, Visual Index), and bear group characteristics (Type, Size, Activity). Some categorical variables were simplified to reduce the number of parameters or when there were too few observations within a given level (Table 3). After reviewing a scatter-plot of the two variables, snow and vegetation cover (%) were combined into a single variable assessing difficulty of detection (Figure 4, Left). Bear-encounter rates did not vary with elevation, so elevation was not considered further (Figure 4, Right).

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Table 5. Top 11 additive covariate models out of the 32 considered, Pilot and Observer data fit separately. Models are ordered by Pilot model weight. Effective search distance is the dominant covariate, with the Pilot and Observer data sets differing in the best additional covariate (Date or Year).

Covariates[a]	Pilot ΔAIC	Pilot model weight	Observer ΔAIC	Observer model weight
ln(ESD) + date	0	0.263	1.82	0.125
ln(ESD) + year	1.10	0.152	0	0.309
ln(ESD) + date + year	1.23	0.142	1.77	0.128
ln(ESD) + date + activity	1.80	0.107	2.26	0.100
ln(ESD) + date + date^2	1.97	0.098	3.82	0.046
ln(ESD) + date + year + date : year	2.33	0.082	3.60	0.051
ln(ESD) + date + year + activity	3.15	0.055	2.84	0.075
ln(ESD) + date + activity + date^2	3.75	0.040	4.24	0.037
ln(ESD) + date + year + activity + date : year	4.19	0.032	4.22	0.037
ln(ESD)	5.16	0.020	3.55	0.052
ln(ESD) + activity	6.91	0.008	4.15	0.039

[a] ln = natural logarithm. ESD = effective search distance.

No significant trends were detected in daily bear group encounter rate (trend P values > 0.30). In both years green-up rapidly advanced throughout the survey period, with leaf-out beginning at low elevation and on southern exposures and rapidly moving upslope. By the end of each survey period, green-up had advanced to the point that visibility declined by more than 50% in riparian areas and on alder *Alnus* slopes. Date was used in the scale function with both linear and quadratic terms in order to account for a temporally increasing then decreasing trend in detections independent of other covariates.

For both the pilot and observer models, logarithm of the effective search distance [ln(ESD)] was the most important covariate when considering just single-covariate models (Table 4). In addition to ln(ESD), the top single covariates for pilot were Date, Year, and Group Activity (Revised, Alternative 2). For observer the additional top covariates were Group Activity (Revised, Alternative 2), Group Activity (Original), and Date. Of the two Activity covariates, only Group Activity (Revised, Alternative 2) was retained given its better performance. Analysis then focused on models with combinations of the covariates ln(ESD), Group Activity (Revised, Alternative 2), Date, and Year.

In addition to the 16 models formed from all possible combinations of these four covariates, consideration was also given to (i) the eight models formed by taking the models with a linear Date term and adding a quadratic term, Date^2, and (ii) the eight models formed by including an interaction between Year and Date or Date^2. Each of the resulting 32 possible additive models were fit independently to each of the two data sets (pilot, observer). The same 11 models had AIC model weights > 0.001 for both the pilot and observer data sets (Table 5).

Combined pilot and observer models. We examined 121 combinations of pilot and observer models. Parameter estimates for the best model are in Table 6. The next best 10 models gave almost identical density estimates, and confidence intervals, obviating any value in conducting multimodel inference (Burnham and Anderson 2002). All parameter estimation calculations converged and no computational problems were encountered.

Maximum probability of detection. Pilots and observers exhibited similar probabilities of detection (Figures 5 and 6). Of bear groups seen by pilot-and-observer teams, pilots detected 69.9 ± 13.4%. Observers detected 71.0 ± 12.1%. Detection rates for individual pilots ranged from 25.0 to 94.7% and observers ranged from 52.4 to 100%. The maximum probability of detection and shape parameters for the best detection functions were relatively precisely estimated from the observations (Table 6). The coefficients for modeling the scale parameters as functions of the covariates were less precisely estimated (Table 6).

Density estimation

Accounting for transect curvature, the total area searched was estimated to be 16,544.42 km^2. Failing to account for transect curvature would overestimate total search area by

Table 6. Parameter estimates for final detection model. The Date covariate did not occur in the Observer model; Year did not occur in the Pilot model.

Parameter	Pilot estimate (SE)	Observer estimate (SE)
Intercept	1.12 (0.65)	0.06 (0.66)
ln(ESD)[a]	0.75 (0.11)	0.90 (0.11)
Date	0.045 (0.016)	
Year effect for 2004		0.27 (0.10)
Shape parameter of detection function	2.96 (0.58)	3.08 (0.48)
Maximum probability of detection	0.89 (0.06)	0.87 (0.06)

[a] ln = natural logarithm. ESD = effective search distance.

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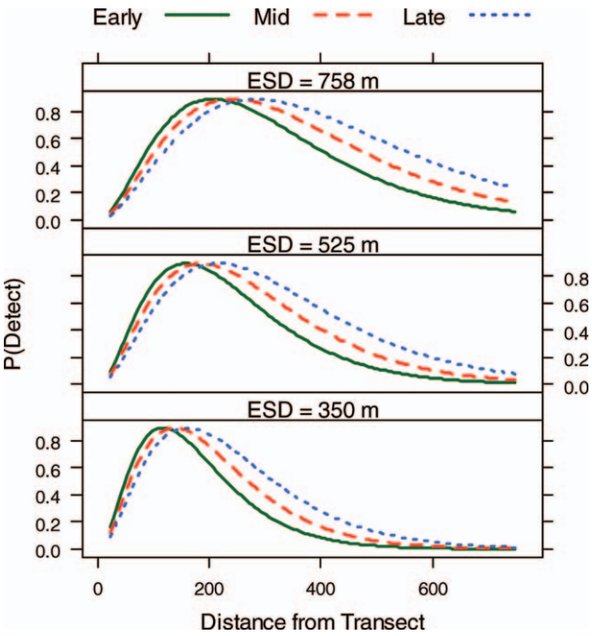

Figure 5. Fitted detection function for pilots (Table 5). Estimated probabilities of detection are plotted at three different effective search distances (the 25th, 50th, and 75th percentiles of the observed effective search distances, corresponding to 350 m, 525 m, and 758 m), illustrating that the peak detection probability increased in distance as did the search distance. The detection model also varied systematically with survey date (classified as Early, Mid, and Late, corresponding to dates 25%, 50%, and 75% through each year's survey period), illustrating that peak pilot detection increased in distance from the transect during the course of the survey period.

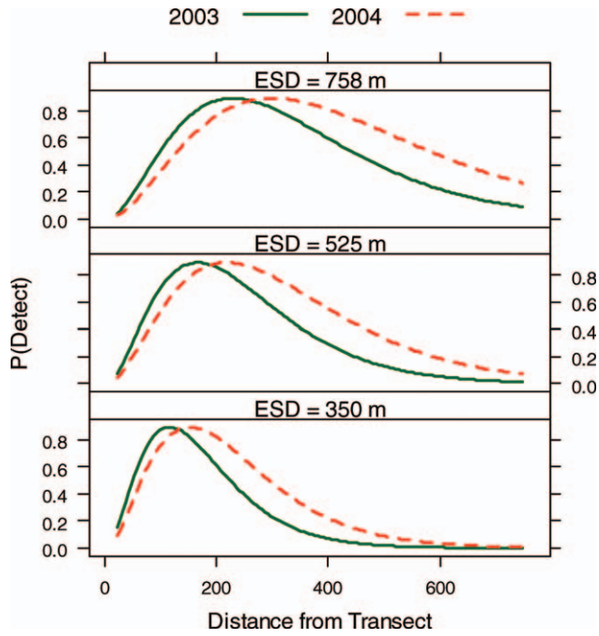

Figure 6. Fitted detection function for observers (Table 5). Estimated probabilities of detection are plotted at three different effective search distances (the 25th, 50th, and 75th percentiles of the observed effective search distances, corresponding to 350 m, 525 m, and 758 m), illustrating that the peak detection probability increased in distance as did the search distance. The detection model also varied systematically with survey year, illustrating that peak observer detection occurred at greater distances in 2004 than in 2003.

5.7%, thus underestimating total density by 1/1.057 = 0.054 or 5.4%. Brown bear population density was estimated as 40.4 bears per 1,000 km^2 (95% CI = 31.4–54.5 and SE 5.1, CV 0.13). The population density of independent brown bears was estimated as 27.3 bears per 1,000 km^2 (95% CI = 21.4–34.4 and SE 3.2, CV 0.12).

Change detection. Minimum change since the current survey detectable with 80% power was estimated at three Type I error rates (Table 7). Using a Type I error rate of 20% allows detection of a minimum change of 38%. To detect population change between surveys, smaller annual rates of change are required as time increases.

Demographics

Because no covariates describing group characteristics were included in the final detection function, the observed bear groups were considered a simple random sample of the bear population. Female and offspring groups constituted 26% of the detected groups (Table 8). These were composed of approximately 26% females with cubs of the year (SE 6.2%), 34% females with yearling cubs (SE 6.6%), and 40% females with cubs 2 y old or older (SE 7.1%). No inferences are made on demographics of the other bear group types reported in Table 8, because we are uncertain of the accuracy of those classifications.

Time requirements

The time necessary for design, implementation, and analysis for this study totaled approximately 3,292 h (*Supporting Information*, Table S3; http://dx.doi.org/10.3996/062009-jfwm-006.S2). Time requirements included approximately 200 h for debugging, modifying, and documenting the analysis code. The total complement of personnel directly involved in this study was 10 pilots, 9 biologists, 1 computer technician, and 2 biometricians.

Discussion

Consistency with previous density estimates

The population density estimate derived here generally agrees with previous work in the area, though these are the first estimates that include standard errors. Miller (1993) suggested that the study area population density was < 40 brown bears/1,000 km^2; Van Daele et al. (2001) hypothesized that the population density of the north-central portion of the study area was approximately 36 bears/1,000 km^2. However, we are likely underestimating true bear population density, because sloping terrain was not considered in calculating total search area.

Demographics–reproduction

Demographic results are subject to at least two potential biases: relatively reduced detection rates for sows with cub of the year, due to changes in behavior and habitat preferences, and undercounting of cubs when a sow and cub group is detected, due to cub size and behavior. The former bias would influence the composition estimates of offspring type per female, but not the mean litter-size estimates (Table 8). While group type was not found to be a useful predictor of detection (Table 4), the composition estimates for offspring per female was opposite that expected in a steady-state population: cubs

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Table 7. Minimum brown bear population change necessary for detection since this survey, at different alpha levels (power = 80%). The underlying population change (λ) is presented for different survey intervals (population decrease, increase).

Alpha	$\lvert\mu_0 - \mu_t\rvert$	Minimum % change	λ 3 y	λ 5 y	λ 10 y
0.05	20.33	50	0.79, 1.21	0.87, 1.13	0.93, 1.07
0.10	18.04	45	0.82, 1.18	0.89, 1.11	0.94, 1.06
0.20	15.40	38	0.85, 1.15	0.91, 1.09	0.95, 1.05

of the year: 26% (SE 6.2%), yearling cubs: 34% (SE 6.6%), and cubs ≥ 2 y old: 40% (SE 7.1%). However, the estimates are not distinguishable given their associated uncertainties, limiting further interpretation.

Undercounting of cubs appears to have occurred in applications of this method to other brown bear populations (E. Becker, Alaska Department of Fish and Game, personal communication). Such bias could affect the estimates of both average litter size of cubs of the year and proportion of offspring by age class (Table 8). The lack of any consistent trend from mean number of cubs per female to yearlings to 2-y-olds, either overall or within a study year, suggests that any bias is negligible relative to the precision of the estimates (Table 8). Additionally, comparing our estimates to those from similar areas or time periods suggests that undercounting is likely negligible relative to the associated uncertainties. The average spring litter size for cubs of the year, for the years 1993–2003, in an area that includes the north-central portion of our study area was 2.0 (SE 0.08; Kovach et al. 2006). Litter sizes from seven other interior Alaska study areas ranged from 1.8 to 2.2 (Kovach at al. 2006). Our study's estimate of 2.0 (SE 0.20) strongly agrees with both sets of results (Table 8). Our study's estimated mean litter sizes for yearling and 2-y-olds, respectively, 2.0 (SE 0.15) and 2.0 (SE 0.20) are somewhat higher than those reported by Kovach et al. (2006), 1.6 (SE 0.08) for yearlings, 1.6 (SE 0.09) for 2-y-olds, and 1.5 (SE 0.19) for 3-y-olds, though not distinguishable considering the associated uncertainties.

Study timing and implementation

The study may have been initiated prior to full den emergence given that brown bear sows in the Kuskokwim Mountains of southwest Alaska have been recorded in dens as late as 31 May (Togiak National Wildlife Refuge, unpublished data) and that in 2003 one of 21 radiocollared sows remained in her den until 19 May (Togiak National Wildlife Refuge, unpublished data). Because of rapid changes in plant phenology in late May and early June, delaying the study would have resulted in decreased detectability and, thus, a greater time investment necessary to attain the minimum sample size.

Extending the data collection in this study across 2 y introduced the unavoidable possibility of population change across years and, thus, formally invalidating the closed-population assumption. However, given the low rate of population change found in brown bears in a similar area 1993–2002 (Kovach et al. 2006), we assume a negligible change in population size during the study period. This is reinforced by the almost identical encounter rates and sizes of bear groups across study years (Table 2), suggesting any changes were minor relative to the precision of the estimates.

Logistics and data management

Learning requirements for conducting this study entailed a significant investment of time. This study required advanced knowledge of GIS and database applications, training in study operations as well as data management, and access to numerous computer applications developed by the Alaska Department of Fish and Game. The analysis required a Master's level familiarity with statistical models, model selection, numerical algorithms, and bootstrap methods.

Application as a monitoring tool

The uncertainty in the density estimates stems from two factors—uncertainty in selecting and fitting the detection function, and variation in bear group size. Uncertainty in the detection function will likely decrease through time as bear group encounters accumulate, from both current and past surveys, and potentially can be used in the model selection and fitting. For example, if the study is repeated at a future date and another 200 groups detected, then all 397 detections can potentially be used in the fitting process. Unfortunately, we have no control over encounter rate or variation in bear group size.

Power analysis indicates that at the existing level of survey effort, and with similar estimate uncertainty, the method can only detect total population change between two surveys of 38% or larger (Table 7). This level of power is less than needed

Table 8. Composition of brown bears groups detected during the survey by year. Standard errors (SE) for percent of total are from 2,000 nonparametric bootstrap resamples; SE for average number of offspring per female are from usual formula for a sample mean.

	2003	2004	Total	Percent of total (SE)
Large males	21	9	30	15 (2.6)
Unknown adult bear groups	27	26	53	27 (3.1)
Breeding pairs	12	17	29	15 (2.5)
Subadult bear groups	11	24	35	18 (2.8)
Female with 2+-y-old cub groups	10	10	20	10 (2.2)
Female with 1-y-old cub groups	8	9	17	9 (2.0)
Female with cub-of-the-year groups	10	3	13	7 (1.8)
Average number 2+-y-olds/female (SE)	2.0 (0.33)	1.7 (0.21)	2.0 (0.20)	
Average number yearlings/female (SE)	1.8 (0.25)	2.2 (0.15)	2.0 (0.15)	
Average number cubs/female (SE)	2.1 (0.23)	1.7 (0.33)	2.0 (0.20)	

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to address current management needs for the Togiak Refuge (i.e., changes of ~ 20% or less over 5 y). Thus, while the method currently has limited value for monitoring bear populations similar to that of the study area, it shows promise for populations of greater density with equal or greater detectability. Based on density estimates (Miller 1993), this potentially includes all nonforested habitat in the coastal regions up to ~ 100 km inland from the Alaska Peninsula to the panhandle region in southeastern Alaska.

Supporting Information

Text S1. Data processing procedures and results.

Table S1. Common problems in data recording and corrective action taken during data cleanup stage.

Table S2. Differences in computer-generated and hand-drawn distance calculations.

All found at DOI: 10.3996/JFWM-006.S1 (55 KB DOC).

Table S3. Survey time requirements by activity.

Found at DOI: 10.3996/JFWM-006.S2 (35 KB DOC).

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