Analysis of 2005 and 2006 Wolverine DNA Mark-Recapture Sampling at Daring Lake, Ekati, Diavik, and Kennady Lake, Northwest Territories

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1. Abstract

This report provides a summary of DNA mark-recapture results for wolverines at Daring Lake, Ekati, Diavik and Kennady Lake in 2005 and 2006. The objectives of analyses were to provide yearly population and density estimates for each study area, provide preliminary estimates of trend, explore factors associated with trend, and conduct power analyses to determine optimal monitoring strategies. The results of analyses demonstrate the utility of DNA sampling in estimating population size, trend and demographic parameters of wolverine populations. Most notably, the high trappability of wolverines at DNA posts makes it possible to obtain precise population estimates with comparatively low survey effort (compared to other carnivore species). Population estimates were very precise despite low numbers of wolverines on some of the study areas. Demographic analysis results suggest that male and female wolverines display unique demography. Male wolverines display larger movements on grids, lower apparent survival and higher immigration/addition rates. Demographic estimates and population estimates suggest that male wolverines population are declining on all study areas, which is potentially influenced by higher rates of harvest. In contrast, females show higher rates of apparent survival, lower rates of movement and immigration into grid area and lower rates of harvest. Female populations appear to be more stable compared to male populations. The results of demographic analysis are challenged by only 2 years of monitoring data. This is the minimal number of time points to determine a trend, and at least 3 to 4 surveys are needed to verify the relationships suggested by the Pradel model demographic analysis. Results of power analyses suggest that sampling can be reduced to biannual effort after 2 or 4 years with minimal loss of power over annual efforts. This study demonstrates that the use of post-sampling and genotyping of harvested wolverines combined with sex-specific demographic analysis provides a powerful method to estimate trend and explore factors affecting demography of wolverine populations. It is our opinion that the DNA-based methodologies presented in this report provide a much more powerful and robust tool for monitoring wolverine populations than track count methodologies. Use of multiple study areas (including the "control" Daring Lake area) allows further inference on causes of local population change and the overall scale of population trend estimates.

2. Introduction

This report provides a summary of DNA mark-recapture results for wolverines at Daring Lake, Ekati, Diavik and Kennady Lake in 2005 and 2006. The objectives of this analysis were as follows:

1. Provide population estimates for each area sampled for 2005 and 2006.
2. Provide preliminary estimates of population trend and explore factors influencing trend for each of the areas.
3. Provide density estimates for each area sampled.
4. The ultimate objective of efforts is to monitor demography over multiple years. We conduct power analyses to explore optimal sampling designs for trend monitoring.

3. Methods

3.1. Field methods

Boulanger et al. (2005) and Mulders et al. (2007) conducted a detailed analysis of previous DNA sampling efforts at Daring Lake. From this work, a design with 1 bait post in a 3x3 km cell sampled for 2 10 day sessions was determined to strike a reasonable balance between logistical effort and mark-recapture model performance. Sampling was conducted on Daring Lake, Diavik, Ekati and Kennady Lake sampling grids, which deployed 284, 141, 118, and 175 posts per session. The number of posts and configuration of sampling was changed for the Ekati grid in 2006 so that 133 posts were sampled (Figure 1).

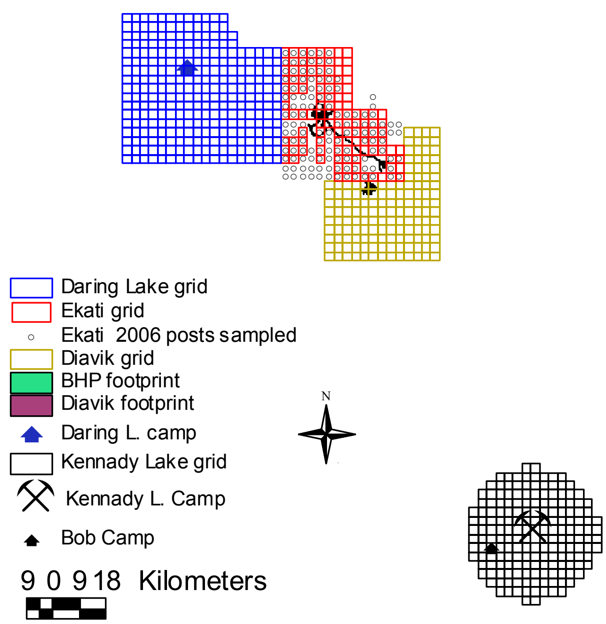

Figure 1: Arrangement of Daring Lake, Ekati, Diavik, and Kennady Lake DNA grids. One post was placed in each cell for all grids with the exception of Ekati in 2006 where the actual posts sampled is noted.

3.2. Population estimation and trend estimation

Samples were genotyped using methods detailed in Mulders et al. (2007) and Paetkau (2003). Only one sample was genotyped per bait post per session. Population size and trend for the 2005-6 data was estimated using the Robust design (Pollock and Otto 1983) Pradel model (Pradel 1996) in program MARK (White and Burnham 1999). Population size and capture probability (p*) were estimated for each year using the Huggins closed population size model (Huggins 1991) and the change in population size (λ) as well as apparent survival (ϕ) and rates of additions between years (f) was estimated using the Pradel model. Apparent survival (ϕ) is the probability that a wolverine that was on the grid in 2005 would still be on the grid in 2006. It encompasses both deaths and emigration from the sampling grid. Rates of addition (f) is the number of wolverines on the grids in 2006 per wolverine on the grid in 2005. It encompasses both births and immigration of wolverines from outside the grid area between the time in which sampling occurred. Apparent survival and rates of addition are added together to estimate change in population size (λ) for the interval between each sampling occasion. Population rate of change is equivalent to the population size for a given sampling period divided by the population size in the previous sampling period ($\lambda=N_{t+1}/N_t$). Given this, estimates of λ will be 1 with a stable population, less than 1 if the population is declining and greater than 1 if the population is increasing.

We used a meta-analysis approach (Boulanger et al. 2002) that considered all the sampling grids for 2005 and 2006 for the MARK analysis. This increased estimate precision by combining sample sizes and also allowed us to explore factors affecting demography and capture probabilities (Figure 2) by comparing the demography of each study area. This approach also allowed separation of study-specific trend and demography from overall trends in wolverine populations.

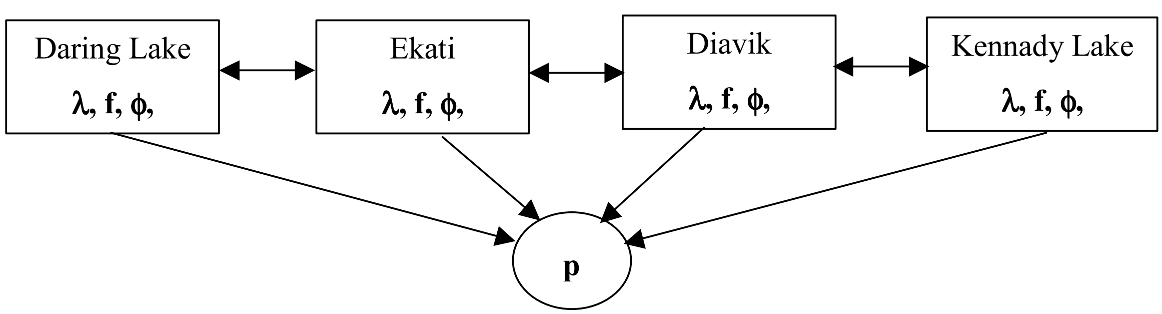

Figure 2: A conceptual diagram of meta-analysis approach to trend monitoring analysis. Data was pooled from study areas to estimate capture probabilities (p). Covariates were used to describe differences in demography (λ-rate of population change, f-rate of additions, and ϕ-apparent survival) between study areas.

Sex and grid were entered as groups in this analysis resulting in 8 groups (2 sexes X 4 grids). Models were built that considered sex-specific, grid-specific and year-specific capture probabilities and demographic parameters. In addition, the area of sampling grids was entered as a covariate based upon the hypothesis that wolverines would show higher fidelity to sampling grids that were larger. We also estimated the proportional removal of harvested wolverines for each grid as the number of wolverines that were identified on grids in 2005 that were harvested (and genotyped) divided by the population estimate for the given sampling grid in 2005. This was done for each sex and entered as a covariate to apparent survival in the analysis.

The fit of models was evaluated using the Akaike Information Criterion (AIC) index of model fit. The model with the lowest AICc score was considered the most parsimonious, thus minimizing estimate bias and optimizing precision (Burnham and Anderson 1998). The difference in AICc values between the most supported model and other models (ΔAICc) was also used to evaluate the fit of models when their AICc scores were close. In general, any model with a ΔAICc score of less than 2 was worthy of consideration.

Population size was also estimated using the Lincoln-Peterson estimator (Lincoln 1930). These estimates were compared with the MARK estimates to explore gains in precision with the meta-analysis approach.

3.3. Estimation of density

It was very likely that closure was violated to different degrees given the different sizes of sampling grids. Therefore, density of wolverines was estimated to allow further comparison of sampling areas. Program DENSITY (Efford 2004, Efford et al. 2004, Efford et al. 2007) was used to estimate density. Program DENSITY estimates the spatial dispersion of wolverines that are captured repeatedly to estimate the amount of area that wolverines covered during sampling, as well as home range centers for wolverines. Using this information, the capture probabilities of wolverines at their home range center (g_0), spatial dispersion of movements (σ) around the home range center, population size, and density are estimated. The actual shape and configuration of the sampling grid is used in the estimation process therefore accounting for the affect of study-area size and configuration on the degree of closure violation and subsequent density estimates. We used a recently developed form of DENSITY that uses a maximum likelihood approach to estimate model parameters (Efford et al. 2007). This approach has the advantage that data from multiple studies can be considered simultaneously. In collaboration with Murray Efford (Program DENSITY author, Zoology Department, University of Otago, New Zealand), we built models that allowed capture probabilities at home range center (g_0), and spatial dispersion of movements (σ) to be similar for each sex across study areas. This allowed pooling of information from each study area with resulting gains in precision. This model was tested against more general models with sex and area specific g_0 and σ estimates. Fit was evaluated using AICc methods as was done with the MARK analyses.

3.4. Exploration of trend monitoring strategies

We used Monte Carlo simulation with Pradel model robust design (as in previous analysis) to explore how much effort would be required to detect change in wolverine population One of the principal questions was whether it is necessary to sample annually to detect change in population size. For example, once the majority of wolverines are genotyped in a study area (i.e. after a few years of surveys) then perhaps the survey effort can be reduced to bi-annual surveys. To explore this further designs were simulated in which surveys were bi-annual after 2 or 4 years of initial surveys (Table 1).

Table 1: Sampling designs simulated.

Design	Simulations	Years sampled 1	2	3	4	5	6	7	8	9	10
1	Annual	x	x	x	x	x	x	x	x	x	x
2	bi-annual after 2 yrs	x	x		x		x		x		x
3	bi-annual after 4 yrs	x	x	x	x		x		x		x

Parameters for simulations were based upon estimates from the robust design Pradel model analysis with 2 years of data from this study as well as estimates from the 3 years of monitoring data at Daring Lake. Simulations were run for initial population sizes of 20, 40, and 80 wolverines which was the range of wolverines estimated on a single grid (20) and all grids combined (80). An even sex ratio of wolverines was assumed. Models that assumed sex-specific demographic rates were used for data generation. Models that assumed sex-specific or pooled demographic rates were used for estimation of parameters. All simulations were conducted using the program MARK simulation module.

Estimates of λ (symbolized as $\hat{\lambda}$) from Pradel models were evaluated in terms of percent relative bias, coefficient of variation, and confidence interval coverage. Percent relative bias is an estimate of bias standardized for the magnitude of the true parameter value (λ).

$$P.R.B. = \frac{\hat{\lambda} - \lambda}{\lambda} \times 100$$

Percent relative bias should be approximately ± 5% for an estimate to be considered unbiased. Coefficient of variation is an estimate of precision in which the standard error of an estimate is divided by the estimate to standardize error for the magnitude of the estimated value. The standard error of $\hat{\lambda}$ was determined by the standard deviation of $\hat{\lambda}$ from replicated simulated trials divided by the mean estimate of λ from replicated trials.

$$CV(\hat{\lambda}) = \frac{S.E.\left(\hat{\lambda}\right)}{\hat{\lambda}} \times 100$$

Coefficient of variation should be less than 10% for estimates of λ if an estimator is considered to be precise enough for use in management.

A z-test test was used to determine power to detect a difference in trends from that of a stable population with λ=1 (Anderson et al. 1995). The null hypothesis for this test is λ=1 and the alternative hypothesis is λ≠1.

$$Z = \frac{1 - \hat{\lambda}}{SE(\hat{\lambda})}$$

Z was distributed as a normal variate. For all simulations α, the type 1 error rate was set to 0.2. The proportion of tests which rejected the null hypothesis of $\lambda=1$ (given true known values of λ) was used as an estimate of power. At least 500 simulations were run for all simulation treatments.

4. Results

4.1. General results

In general, sampling for wolverines was very effective with most individuals being captured multiple times in each of the study areas (Table 2). Multiple captures were tallied by considering the number of different captures of an individual at different bait posts during different sessions. For example, at Daring Lake in 2005 both male and female wolverines were captured on average 8.4 times with some females being captured up to 36 times. Information from multiple captures was used to model capture probability variation and estimate density.

Table 2: Statistics for the number of captures of unique individuals for the duration of sampling as a function of sex and area sampled

Area	Sex	Individual captures									
		2005					2006				
		Mean	Std	n	Min	Max	Mean	Std	n	Min	Max
Daring Lake	Female	8.4	9.4	17	1	36	9.6	8.9	16	1	33
	Male	9.1	9.0	21	1	27	10.6	11.6	17	1	44
	Pooled	8.8	9.1	38	1	36	10.1	10.2	33	1	44
Diavik	Female	3.1	1.9	13	1	7	5.6	5.6	14	1	23
	Male	8.9	11.1	11	1	37	7.9	9.7	8	1	29
	Pooled	5.8	8.0	24	1	37	6.4	7.2	22	1	29
Ekati	Female	4.1	2.4	9	1	8	4.4	3.7	9	1	11
	Male	5.5	3.9	12	1	14	5.6	3.5	5	2	9
	Pooled	4.9	3.4	21	1	14	4.9	3.5	14	1	11
Kennady Lake	Female	12.8	9.2	9	2	33	6.6	4.9	11	1	16
	Male	4.6	4.3	8	1	14	5.3	8.3	6	1	22
	Pooled	8.9	8.3	17	1	33	6.2	6.1	17	1	22

Multiple captures of individuals within sessions were pooled for mark-recapture analysis. Summary statistics and capture probability estimates (Table 3) suggested that sampling was highly efficient with capture probabilities above 0.5 for all projects. These results suggest that the Lincoln Peterson estimator or simpler mark-recapture models should be reasonably robust to capture probability variation (due to the high capture probabilities of wolverines).

Table 3: Summary statistics for 2005-6 sampling grids. Estimates are summarized by area and sex. The number of wolverines captured in the first session (n1), second session (n2), number of wolverine caught in both session (m2), number of total individual wolverines captured (M_{t+1}), and Lincoln Petersen model estimates of capture probability.

Area	Sex	Year	Wolverines captured				Capture probability
			Individuals	1st session	2nd session	Both	
Daring	Females	2005	17	12	14	9	0.70
		2006	16	14	13	11	0.82
	Males	2005	21	17	17	13	0.76
		2006	17	11	17	11	0.82
	Pooled	2005	38	29	31	22	0.73
		2006	33	25	30	22	0.81
Diavik	Females	2005	13	12	7	6	0.68
		2006	14	9	13	8	0.75
	Males	2005	11	10	7	6	0.73
		2006	8	6	6	4	0.67
	Pooled	2005	24	22	14	12	0.70
		2006	22	15	19	12	0.72
Ekati	Females	2005	9	7	7	5	0.71
		2006	10	10	4	4	0.70
	Males	2005	12	10	11	9	0.86
		2006	8	6	6	4	0.67
	Pooled	2005	21	17	18	14	0.80
		2006	18	16	10	8	0.65
Kennady	Females	2005	9	8	9	8	0.94
		2006	11	8	11	8	0.86
	Males	2005	8	3	7	2	0.48
		2006	6	3	5	2	0.53
	Pooled	2005	17	11	16	10	0.77
		2006	17	11	16	10	0.77

Some wolverines were captured on more than 1 sampling grid due to the close proximity of the Daring Lake, Ekati and Diavik grids. Notably, 3, 2, and 1 female were captured on the Daring Lake-Ekati, Daring Lake-Diavik, and Ekati-Diavik grids respectively. For males, 4 and 2 were captured on the Daring Lake-Ekati and Ekati-Diavik grids respectively.

Table 4 summarizes known mortalities (harvested) of individuals previously identified in the post samples. Some samples were collected after the 2006 DNA sampling. All mortalities were male except at Daring Lake where 1 female was harvested between 2005 and 2006 and 2 females were harvested after 2006 DNA sampling efforts. Two males were harvested that were detected in post samples on both the Ekati and Diavik grids and these are categorized as Diavik-Ekati in Table 4.

Table 4: Summary of wolverines captured in post samples that were harvested (and carcass sample genotyped). All wolverines were male except those noted in parenthesis that were female. Two male wolverines that were captured on both the Ekati and Diavik grids were harvested and these are categorized under Diavik-Ekati. The interval corresponds to when the carcass was collected relative to DNA post sampling

Project	2005-6	After 2006[A]	Grand Total
Daring	3 (1)	0 (2)	6
Diavik	1	0	1
Diavik-Ekati	1	1	2
Kennady	3	0	3
Grand Total	9	3	12

[A]Wolverines were harvested after 2006 DNA sampling occurred

4.2. Summary of wolverine spatial distribution

The distribution of captures of wolverines was indexed by the number of captures at bait posts (Figures 2 and 3). It can be seen that the distribution of wolverines was not uniform with some bait posts receiving no hits but others receiving hits during both sampling sessions. Only one sample was analyzed per post/session and therefore it was entirely possible that some posts received more than 2 hits. The configuration of posts in the sampling grid was slightly different for Ekati in 2006 as noted in Figure 2.

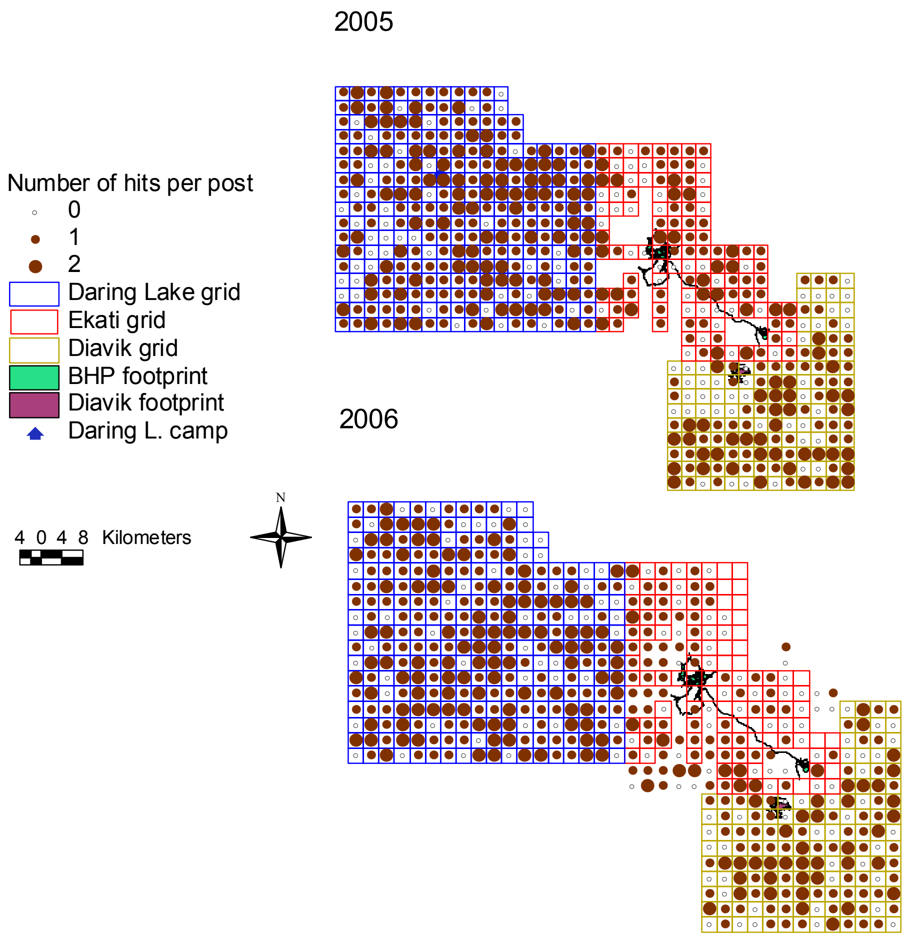

Figure 3: Distribution of wolverines on sampling grids as indexed by the number of captures at bait posts for the Daring Lake, Ekati and Diavik study areas for 2005 and 6. Each bait post could receive up to 2 captures (since only 1 sample per session was analyzed). The posts sampled were different in 2006 in Ekati as noted. Only the posts sampled each year are shown.

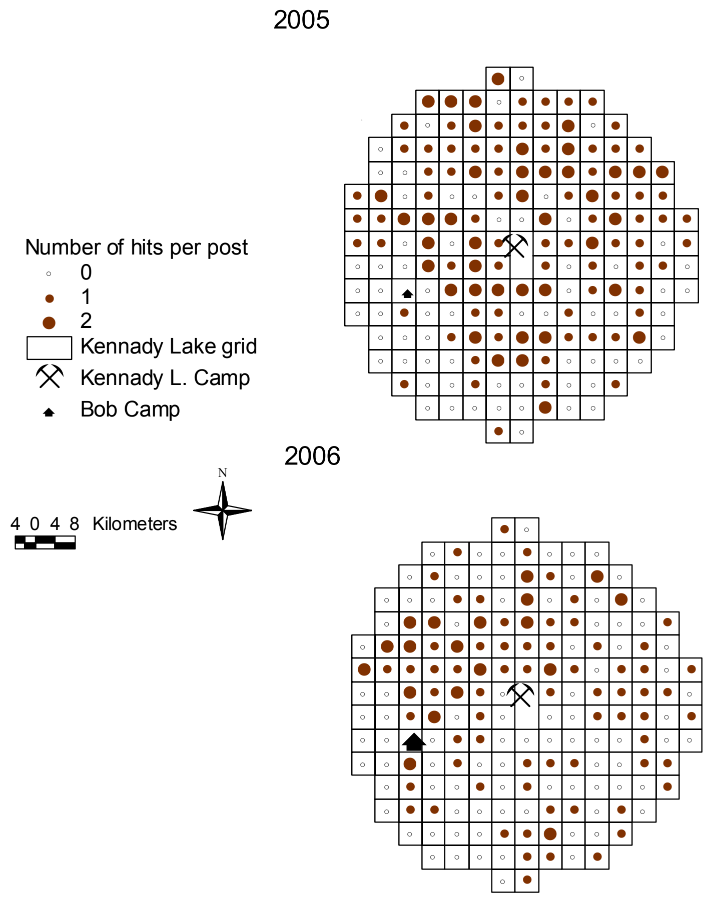

Figure 4: Distribution of wolverines on sampling grids as indexed by the number of captures at bait posts for the Kennady Lake study area for 2005 and 6. Each bait post could receive up to 2 captures (since only 1 sample per session was analyzed).

To explore fidelity and movement of individual wolverines identified in DNA sampling we linked mean capture locations of wolverines that were captured in 2005 and 2006 with lines (Figures 5 and 6). We also noted individuals that were known mortalities. In general, a higher level of fidelity, and minimal movement of female wolverines can be seen based upon a large number of home range centers for individuals that are close together for successive years (linked together by lines in Figures 5 and 6). In contrast, males exhibited larger movements, and more males were only captured for 1 year suggesting higher mortality and/or lower fidelity.

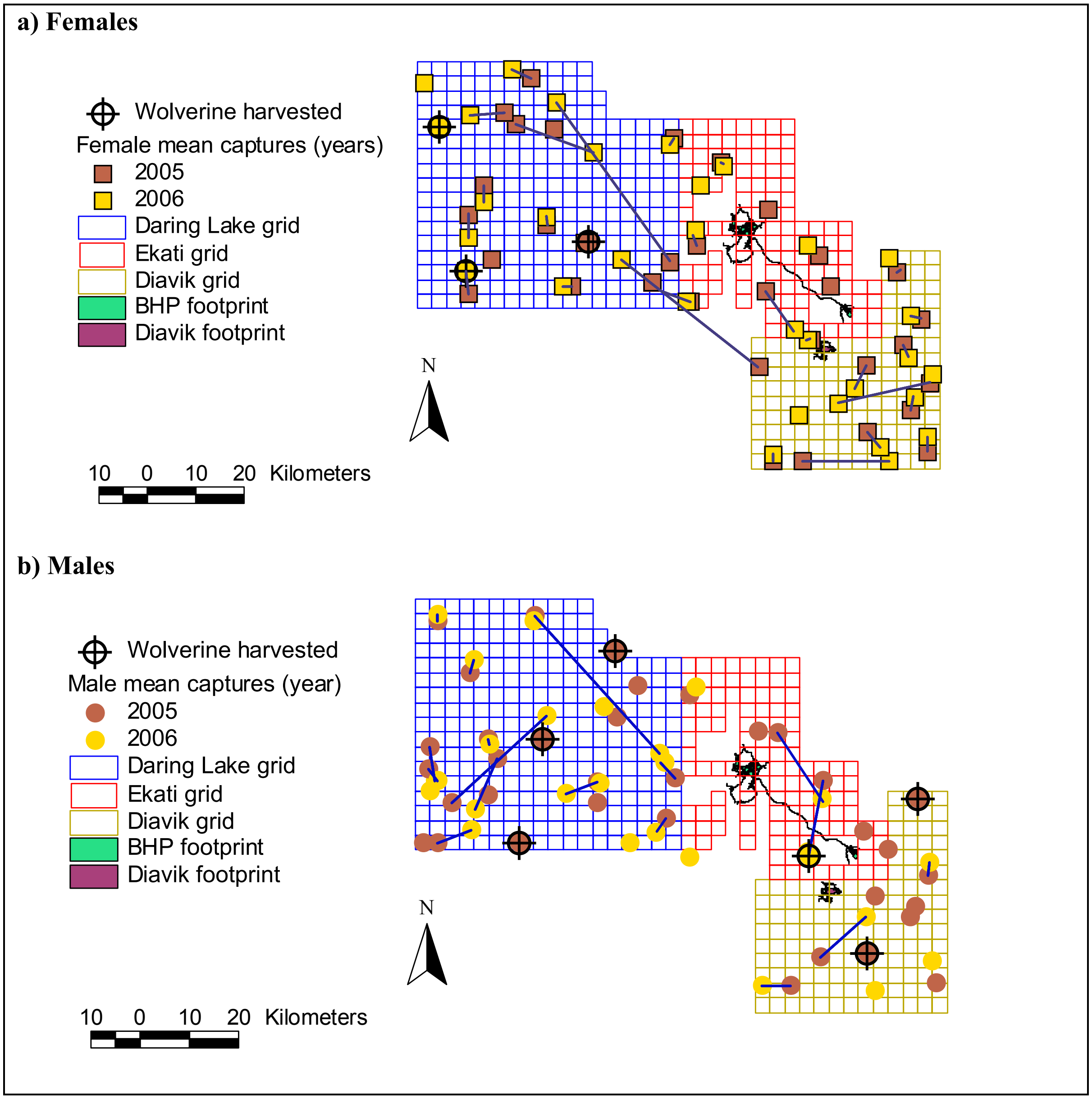

Figure 5: Distribution of wolverines on sampling grids as indexed by mean capture location for the Daring Lake, Ekati, and Diavik study areas for 2005 and 2006. The mean capture locations for wolverines captured in multiple years are connected by a line. A mortality symbol was placed over the home range center for wolverines that were harvested.

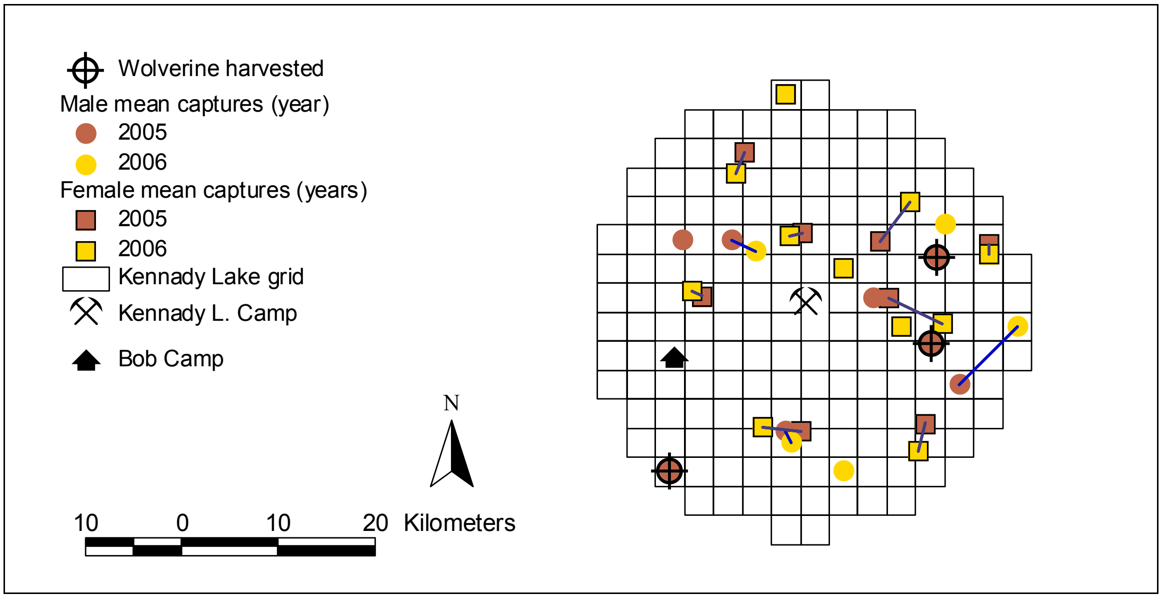

Figure 6: Distribution of wolverines by sex on sampling grids as indexed by mean capture location in 2005 and 6 for the Kennady Lake study areas. The mean capture locations for wolverines captured in multiple years are connected by a line. Wolverines with no lines were only captured in one of the 2 years. A mortality symbol was placed over the home range center for wolverines that were harvested.

4.3. Population size, trend, and demography

The Pradel/Huggins model robust design was used to obtain population estimates and estimates of trend and demography. Results of model selection analysis suggest that apparent survival was most influenced by sex of wolverine and the size of the grid area for male wolverines (Model 1, Table 5). Rates of addition (births and immigration) were also influenced by sex of wolverine. Capture probabilities were similar between sexes as shown by relatively low support of a model with sex-specific capture probabilities (Model 8). In addition there was minimal suggestion of a behavioural response to trapping as indicated by low support of a model with sex-specific capture and recapture rates (Model 15). Many models were supported by data as indicated by delta AICc values of less than 2.

Table 5: AICc model selection for Pradel trend analysis. Akaike Information Criteria (AIC_c), the difference in AIC_c values between the *i*th model and the model with the lowest AIC_c value (Δ_i), Akaike weights (w_i), number of parameters (*K*) and model deviance are presented

No	Apparent survival (ϕ)	Additions (f)	Capture prob. (p*) Recapture prob.(c*)	AICc	ΔAICc	w_i	K	Deviance
1	sex+ GA_{males}[A]	sex	constant	638.8	0.00	0.159	6	626.6
2	sex	sex	constant	640.0	1.09	0.092	5	629.8
3	sex+ GA_{males}	sex+GA	constant	640.1	1.18	0.088	7	625.7
4	sex+ GA_{males}	sex+ GA_{males}	constant	640.1	1.23	0.086	7	625.7
5	sex*GA	sex	constant	640.2	1.36	0.080	7	625.9
6	sex+GA	sex	constant	640.7	1.82	0.064	6	628.4
7	project*sex(F)+ GA_{males}	sex	constant	640.7	1.83	0.064	9	622.1
8	sex+ GA_{males}	sex	sex	640.8	1.87	0.062	7	626.4
9	sex+ GA_{males} + harvest	sex	constant	641.0	2.09	0.056	7	626.6
10	sex	sex+ GA_{males}	constant	641.4	2.48	0.046	6	629.1
11	sex	sex	sex	641.8	2.93	0.037	6	629.5
12	sex+GA	sex+GA	constant	641.9	3.01	0.035	7	627.5
13	sex	sex	year	642.1	3.17	0.032	6	629.8
14	sex	sex	sex+GA	642.5	3.60	0.026	7	628.1
15	sex+ GA_{males}	sex	p*(sex) c*(sex)	642.6	3.73	0.025	9	624.0
16	sex+GA	sex	sex	642.7	3.77	0.024	7	628.3
17	sex*project	sex	constant	644.1	5.20	0.012	8	627.6
18	sex	sex	sex	644.7	5.81	0.009	8	628.2
19	constant	constant	p*(sex) c* (sex)	646.6	7.72	0.003	6	634.3
20	sex+project	sex+project	constant	649.5	10.65	0.001	11	626.6
21	constant	constant	constant	650.7	11.79	0.000	3	644.6
22	constant	constant	p* (.)c* (.)	651.9	13.05	0.000	4	643.8
23	GA	sex	constant	654.2	15.29	0.000	5	644.0
24	project	constant	constant	654.7	15.80	0.000	6	642.4
25	constant	project	project	656.1	17.19	0.000	6	643.8
26	project	project	project	660.1	21.20	0.000	9	641.5
27	project	project	project	665.4	26.52	0.000	12	640.3

[A] GA refers to the area of each sampling grid. The effect of sampling grid area was modeled exclusively for males (GA_{males}) or for both sexes (GA).

Model averaged superpopulation estimates (wolverines that spent time in the study area and surrounding area during sampling) were produced using Huggins models (Table 6). Precision of estimates was good with the coefficient of variation of most estimates being below 10%. Estimates from MARK were close to Lincoln Petersen estimates. One issue with LP estimates was the effect of low number of capture wolverines (Table 3), which prevented estimates of standard error of population size. In contrast, MARK models used information from all projects to estimate capture probability therefore providing more reliable and robust standard error estimates.

Table 6: Model-averaged superpopulation estimates from Pradel/Huggins model robust design analysis. Population estimates ($\hat{N}$) and their associated standard errors (SE) and confidence intervals (CI) are given. In addition Lincoln-Petersen (LP) model estimates and the number of unique wolverines identified (M_{t+1}) or are given for comparison purposes.

Project	Sex	Year	M_{t+1}	MARK					LP		
				$\hat{N}$	SE	CI		CV	$\hat{N}$	SE	CV
Daring Lake	Male	2005	21	23	1.53	22	26	6.8	22	1.33	6.0
		2006	17	18	1.35	17	21	7.4	17		
	Female	2005	17	18	1.22	17	21	6.7	19	1.63	8.8
		2006	16	17	1.18	16	19	6.9	17	0.82	5.0
	Pooled	2005	38	41	2.00	39	45	4.9	41	2.18	5.4
		2006	33	36	1.83	34	39	5.1	34	1.23	3.6
Ekati	Male	2005	12	13	1.12	12	15	8.7	12	0.49	4.0
		2006	8	9	0.90	8	10	10.3	9	1.14	13.0
	Female	2005	9	10	0.87	9	11	9.0	10	1.01	10.4
		2006	10	11	0.92	10	13	8.6	10		
	Pooled	2005	21	23	1.44	22	25	6.4	22	1.07	4.9
		2006	18	19	1.30	19	22	6.7	20	1.92	9.7
Diavik	Male	2005	11	12	1.07	11	14	9.0	12	0.95	8.2
		2006	8	9	0.90	8	10	10.4	9	1.14	13.0
	Female	2005	13	14	1.06	13	16	7.6	14	1.26	9.1
		2006	14	15	1.10	14	17	7.3	15	0.93	6.4
	Pooled	2005	24	26	1.53	25	29	5.9	26	1.71	6.7
		2006	22	24	1.44	23	26	6.1	24	1.69	7.1
Kennady Lake	Male	2005	8	9	0.89	8	10	10.2	10	2.11	21.8
		2006	6	6	0.76	6	8	11.7	7	1.41	20.2
	Female	2005	9	10	0.87	9	11	9.0	9		
		2006	11	12	0.97	11	14	8.2	11		
	Pooled	2005	17	18	1.25	17	21	6.8	18	0.92	5.2
		2006	17	18	1.24	17	21	6.8	18	0.92	5.2

Inspection of population estimates suggests that male estimates declined for most projects between 2005 and 6 whereas female estimates were more stable. We divided known numbers of wolverines harvested from study areas (Table 4) by 2005 population estimates to estimate the percentage of wolverines harvest from each study area. From this we estimate that 8.8%, 16.7%, 7.7% and 34.6% of the 2005 population size of males on the Daring, Diavik, Ekati, and Kennady Lake grids were harvested in the interval between sampling in 2005 and 6. Only 1 female was harvested during this interval on Daring Lake, which represented 5.4% of the estimated 2005 population. These proportions were entered as covariates for apparent survival in the Pradel model analysis, however this model was not supported by the data (Table 5, model 9) presumably due to low power to detect trends in apparent survival with only 2 years of data.

The Pradel model produced estimates of trend as well as demography to allow further investigation of trend. The best way to interpret trend and demographic estimates is through the display of model-averaged estimates that consider estimates from all the models in the analysis (Figure 7). Inspection of estimates suggests that apparent survival and rates of addition was similar for females across all sampling grids. In all cases estimates of λ were greater than 1, however, confidence intervals overlapped 1. In contrast, apparent survival of males was lower and rates of additions was higher. Population trend (λ) was less than 1 for all grids, however, confidence intervals also overlapped 1. These results are relatively imprecise therefore limiting inference. However, they do suggest differences in demography among sexes.

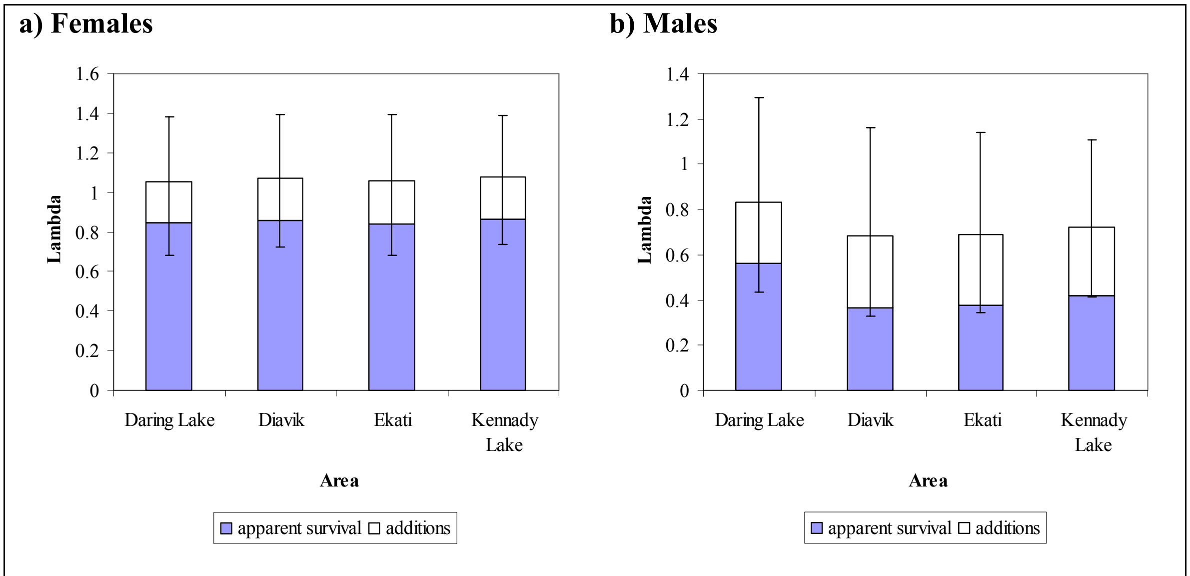

Figure 7: Model averaged estimates of λ, apparent survival and additions from the Pradel model robust design analysis (Table 8). Apparent survival plus additions equal λ (the annual rate of change for the population). Confidence intervals are given for λ.

One way to further interpret demographic estimates is through estimates of seniority which is apparent survival divided by λ (Nichols and Hines 2002). This estimates the relative amount that survival is driving the demography of each sex class. One minus seniority measures the proportional amount that additions influence demography. In this case, mean seniority was 0.8 and 0.58 for females and males respectively. This suggests that apparent survival drives the demographics of females on grids whereas apparent survival and additions both drive the demography of males.

One finding of the Pradel model was the influence of grid size on male demographics (Figure 8). This basically suggests that male fidelity is lower on smaller sampling grids and therefore, the estimated demography of males is scale-dependent. This further highlights the general transient nature of the male segment of the population.

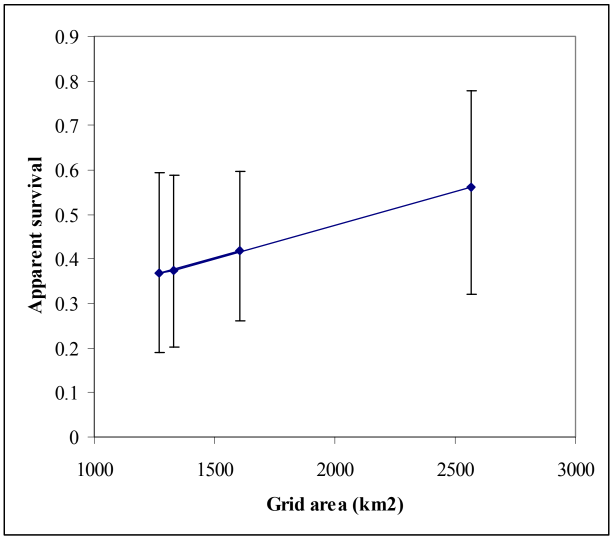

Figure 8: The estimated relationship between apparent survival and grid area for male wolverines from Model 1 (Table 8).

The Pradel model made some restrictive assumptions about factors influencing demography such as grid size and sex-specific variation. We compared estimates of λ from the Pradel model with the estimates of λ from the Huggins model (estimated as the ratio of successive population estimates) (Figure 9). In general, estimates were similar especially when the precision of the estimates was considered.

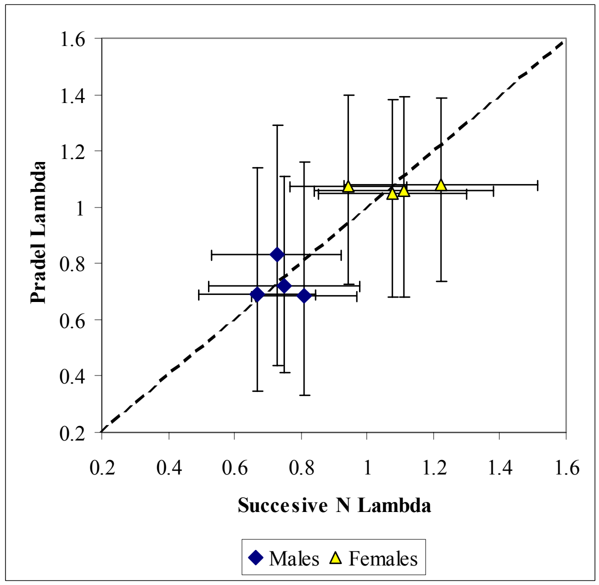

Figure 9: Comparison of estimates of trend (λ=N_{t+1}/N_t) from successive Huggins model population estimates and from the Pradel model. Error bars are 95% confidence intervals for λ estimates.

4.4. Estimates of Density

As an initial step in the DENSITY analysis, movements of wolverines during sampling was summarized and graphically compared for each of the sampling areas. This was done by using a modified version of the Jennrich and Turner 95% ellipse home range area estimator (Jennrich and Turner 1969, Hooge and Eichenlaub 1997). We reduced the estimator to a 50% ellipse so that the area of each ellipse is roughly equal to the spread of post captures for each individual wolverine (Figure 10). Results show a large degree of variation between wolverines with some male wolverines traversing a high proportion of the grid area(s). One factor that affects the actual amount of area traversed as estimated by post captures is the position of the wolverine on the grid. Wolverines near the grid edge probably traversed off grid areas and therefore their areas will be underestimated. Program DENSITY explicitly models wolverine position on grid and its influence on estimated movement therefore minimizing this potential source of bias in estimating movement of wolverines across grid areas.

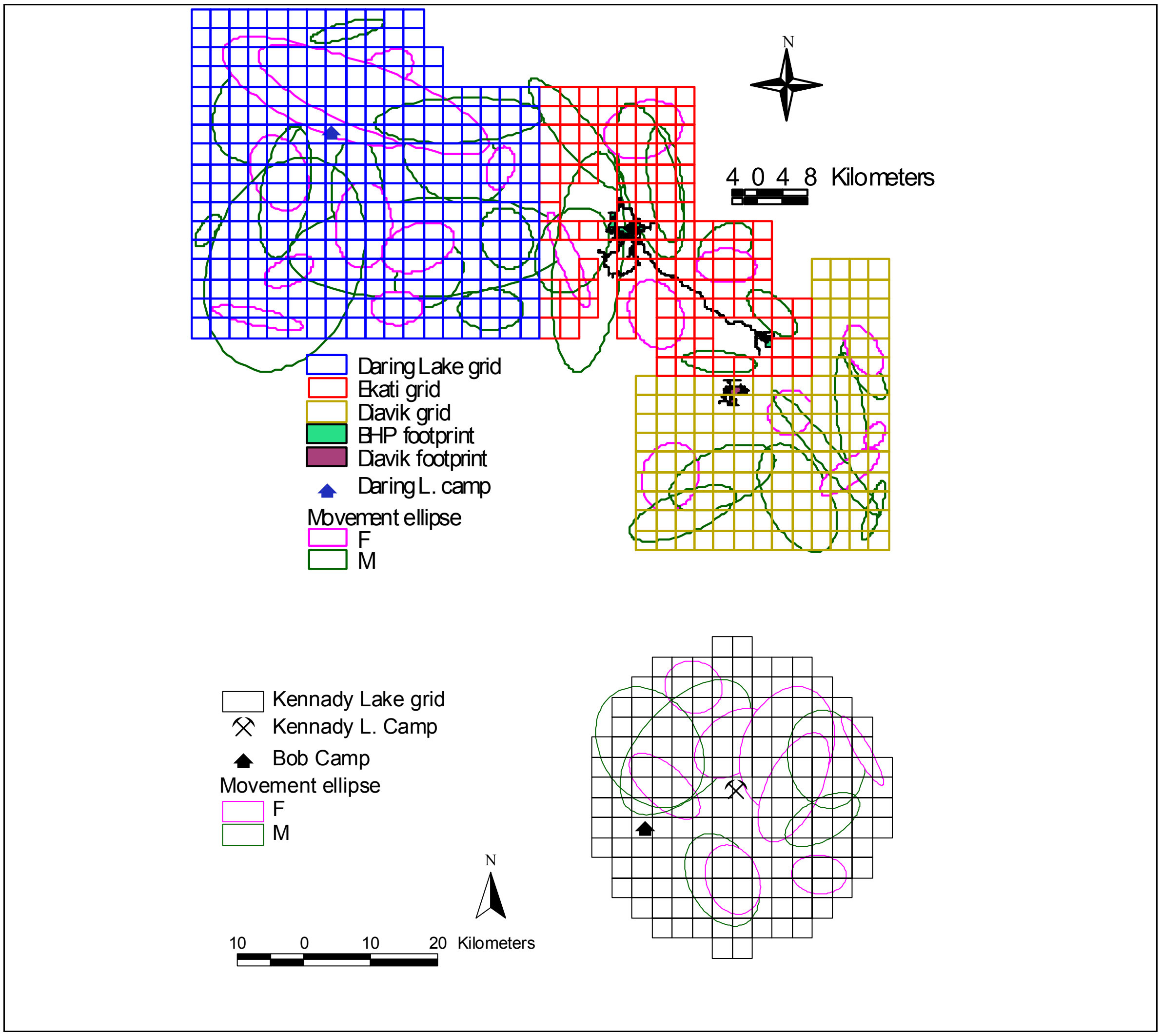

Figure 10: Male (green) and female (pink) wolverine movements during sampling for the Daring Lake, Diavik, Ekati and Kennady Lake sampling grid in 2005. Each ellipse was reduced to 50% so that the size of the ellipse is roughly equal to the spread of repeated captures of each individual.

Model selection results from program DENSITY suggested that capture probability at home range center and dispersion varied by sex, project, and year (Table 7). Estimates of capture probability at home range center (g_o) suggest that capture probability was variable between years and studies, however, interpretation of results was offset by low precision (Figure 11). In contrast, spatial variation was reasonably similar between years with a general tendency of male dispersion to be higher than female dispersion.

Table 7: DENSITY model selection for meta-analysis of 2005-2006 wolverine data. Akaike Information Criteria (AIC_c), the difference in AIC_c values between the *i*th model and the model with the lowest AIC_c value (Δ_i), Akaike weights (w_i), number of parameters (*K*) and log-likelihood of the model are presented.

Capture probability(g_o)	Dispersion (σ)	AICc	ΔAICc	w_i	K	Log-likelihood
sex x study x year	sex x study x year	10099.1	0	1.00	32	-5010.82
sex x study	sex x study	10171.9	72.81	0.00	16	-5068.38
sex	sex	10275.2	176.07	0.00	4	-5133.47
constant	constant	10313.8	214.70	0.00	2	-5154.86

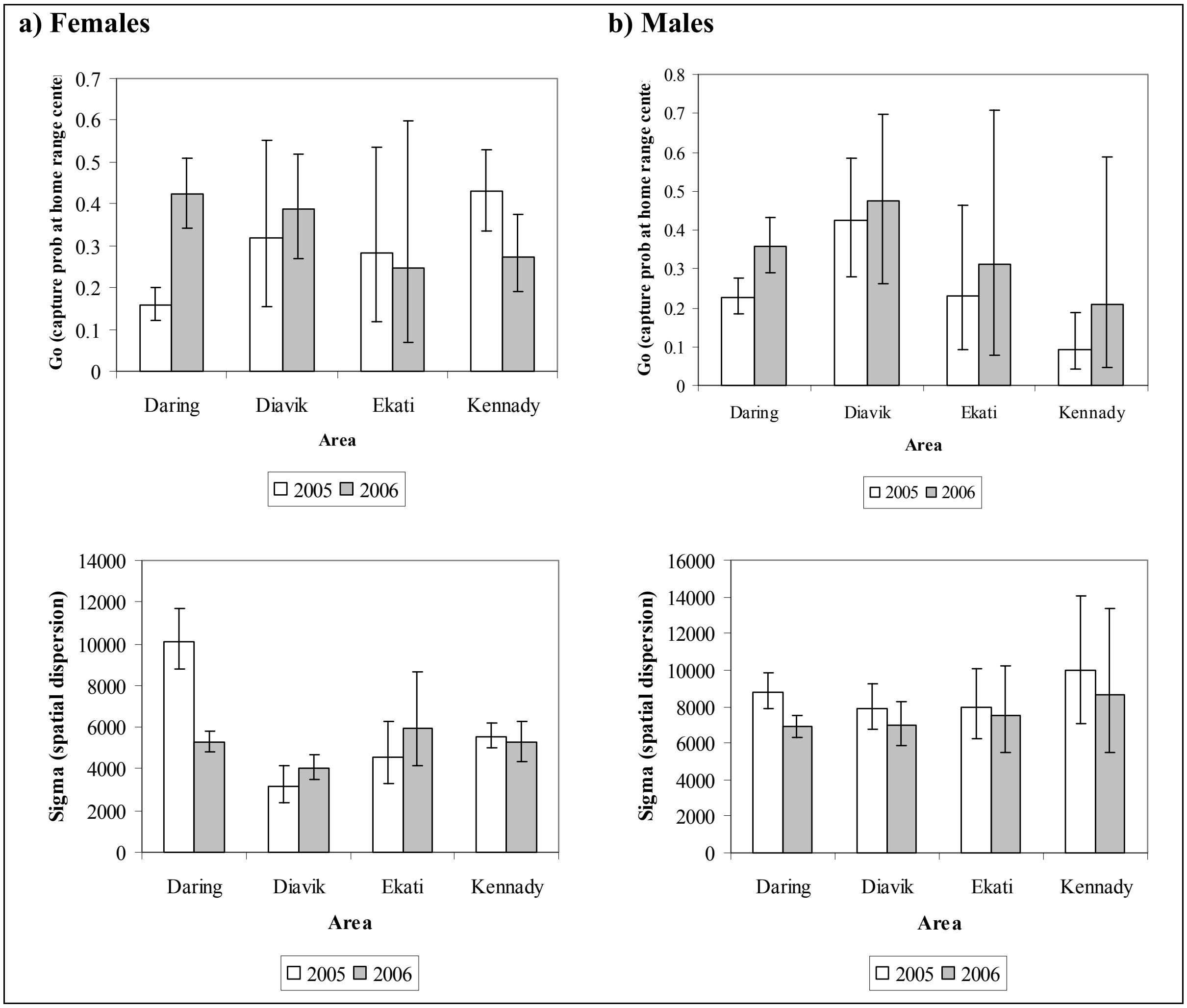

Figure 11: Estimates of capture probability at home range center and spatial dispersion (σ) from the most supported AICc model (Table 6) for females and males.

Estimates suggest higher density of male wolverines in the Daring Lake grid and higher female densities at Diavik (Figure 12). This may seem counterintuitive given that the population estimate was higher for Daring Lake. However, the Daring Lake sampling grid area (2556 km^2) was substantially larger than the Diavik sampling grid (1269 km^2) and therefore a larger population size would be expected. As with population size estimates, female densities were roughly even, whereas male density estimates decreased from 2005 to 2006.

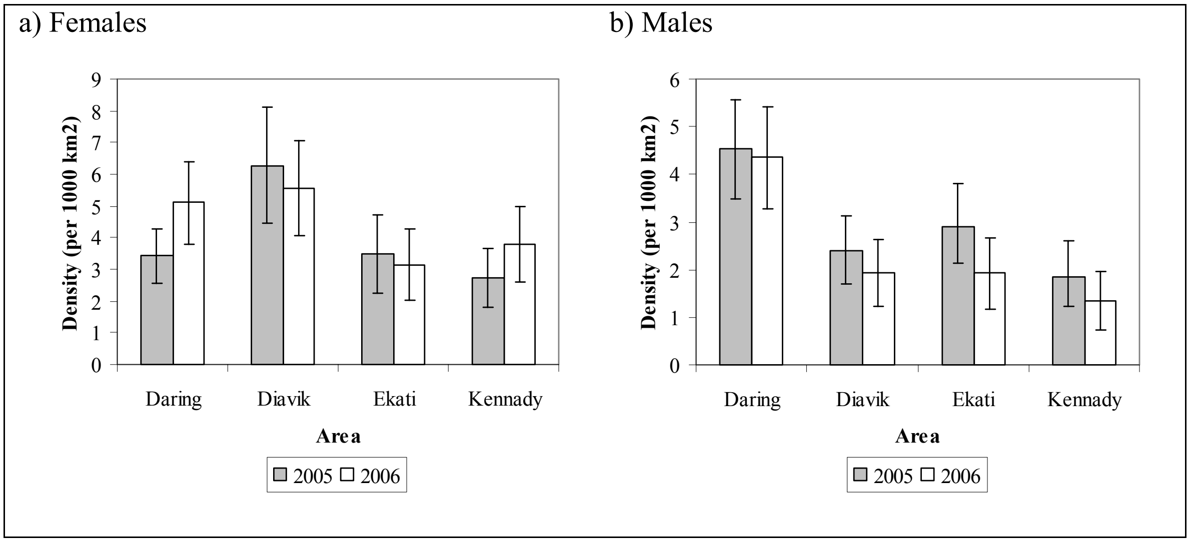

Figure 12: Estimates of density for female (left) and male (right) wolverines for each of the study areas and years sampled. Standard errors of estimates are given as error bars.

The average number of wolverines on the sampling grid at any one time was estimated by multiplying the sampling area by the density estimate (Table 8). From this it can be seen that the average population size on sampling grids was 24-74% of the superpopulation size estimate suggesting substantial violation of closure on sampling grids.

Table 8: Estimates of density (wolverines/1000km^2), superpopulation ($\hat{N}$), and average number of wolverines on the sampling grid (Ave $\hat{N}$) at any one time.

Sampling area			Density		Population size		
Project	Area(km^2)	Year	$\hat{D}$	SE($\hat{D}$)	$\hat{N}$	Ave $\hat{N}$	SE
Females							
Daring	2556	2005	3.424	0.864	18	8.75	1.73
	2556	2006	5.096	1.289	17	13.03	2.59
Diavik	1269	2005	6.283	1.828	14	7.97	3.67
	1269	2006	5.565	1.513	15	7.06	3.04
Ekati	1062	2005	3.473	1.228	10	3.69	2.46
	1197	2006	3.146	1.112	11	3.77	2.23
Kennady	1575	2005	2.735	0.92	10	4.31	1.84
	1575	2006	3.804	1.183	12	5.99	2.37
Males							
Daring	2556	2005	4.541	1.025	23	11.61	2.06
	2556	2006	4.35	1.072	18	11.12	2.15
Diavik	1269	2005	2.392	0.746	12	3.04	1.50
	1269	2006	1.935	0.703	9	2.46	1.41
Ekati	1062	2005	2.886	0.905	13	3.06	1.81
	1197	2006	1.931	0.747	9	2.31	1.50
Kennady	1575	2005	1.849	0.746	9	2.91	1.50
	1575	2006	1.351	0.622	6	2.13	1.25

4.5. Power analysis of trend monitoring strategies

Simulation parameter estimates were based upon the results of the Pradel Robust design analysis (Table 9) and analysis of the 2004-2006 Daring Lake data set.

Table 9: Simulation parameters for Pradel model simulations

Parameters	Males	Females
Apparent survival	0.67	0.76
Rates of addition	0.28	0.19
Lambda	0.95	0.95
Recapture rate	0.73	0.73

Results (Table 10) suggest that the Pradel model was robust to heterogeneity in demographic rates with estimates of λ that had minimal bias. The power and precision of estimates was influenced by initial population size, whether estimates were sex-specific or pooled, and design. In general, there was adequate power to detect an annual 5% change in population size (λ=0.95) for pooled estimates for initial population sizes above 20 regardless of design. Adequate power to detect sex-specific trends was only possible if population size was upwards towards 80, which represents the approximate population size of all the grids sampled.

Table 10: Performance of sampling designs (Table 1) and Pradel model after 10 years of monitoring. Results are given for different initial population sizes (N). Power levels of 0.8 or above are considered adequate for monitoring.

Design Sex	Results Power[A] N=20	40	80	Bias N=20	40	80	CV(λ)[B] N=20	40	80
Annual									
Female	0.64	0.75	0.85	-2.86	-1.19	-0.29	7.81	4.84	3.54
Male	0.65	0.77	0.89	-3.66	-1.65	-1.19	9.54	6.34	3.78
Pool	0.75	0.90	0.96	-1.91	-0.77	-0.40	5.49	3.66	2.47
Bi-annual after 2 years									
Female	0.55	0.66	0.76	0.09	0.83	1.16	6.42	4.19	3.00
Male	0.56	0.63	0.76	-0.51	0.21	0.70	7.31	5.12	3.59
Pool	0.63	0.77	0.92	0.59	0.93	1.16	4.68	3.14	2.17
Bi-annual after 4 years									
Female	0.64	0.71	0.80	-1.68	-0.73	-0.38	9.39	5.85	3.92
Male	0.65	0.68	0.81	-3.33	-2.34	-1.04	10.72	7.54	4.73
Pool	0.75	0.79	0.93	-1.24	-0.94	-0.43	6.53	4.65	2.86

[A]Power to detect decline after 10 years of surveys. Designs summarized in Table 1.
[B]Coefficient of variation

The other factor that affects power is the rate of population decline. We ran exploratory simulations with more rapid rates of decline. We found that adequate power could be achieved to detect a 10% decline for pooled sexes within 6 years even if the initial population size was 20. Sex-specific declines of 15% and 13% could be detected for males and females with an initial population size of 20 in 6 years.

A 20% (λ=0.8) decline was estimated in the male population from the 2 year analysis conducted in this paper. However, confidence intervals for λ overlapped 1 and therefore the decline was not statistically significant. Further simulations suggest that 3 years of monitoring would be needed to statistically detect sex-specific declines if initial population size was 40 and 4 years would be needed to detect sex-specific declines if initial population size was 20.

5. Discussion

5.1. General comments

The results of this analysis demonstrate the utility of DNA sampling in estimating population size, trend and demographic parameters of wolverine populations. DNA-based population estimation methods have been broadly adopted in the management of North American bear populations (Boulanger et al 2002), but have been slow to be taken up in other species, largely because of the challenge of developing efficient methods to collect adequate DNA samples. The post collection system that was developed at Daring Lake in 2003 (Mulders et al 2007), and then applied in this study, represents a major breakthrough not only because it makes this methodology practically available in a new species, but because the estimates obtained in wolverines with this methodology have far higher capture probabilities, and thus greater precision, than what has typically been achieved in other species (Boulanger et al 2002), or using other methods in wolverines (Mulders et al 2007). The other innovation of this project is the application of recent modeling advances in program MARK and DENSITY that allow the pooling of data from all the projects therefore allowing the rigorous comparison of the demography of projects as well as more precise parameter estimates. One immediate benefit of this is that we were able to produce precise population estimates using just 2 sessions per year, instead of the 4 to 5 sessions that are more typically used. We were also able to estimate trends, model sex-specific and sampling area-specific demography, albeit with low statistical confidence, that would not be observable with the wider confidence intervals that are more commonly observed.

One of the most interesting results is that male and female wolverines display unique demography. Male wolverines display larger movements on grids as estimated by program DENSITY (Figures 10 and 11), lower apparent survival and higher immigration/addition rates (Figure 7) as estimated by the Pradel Model robust design analysis. Demographic estimates and population estimates suggest that male wolverines population are declining on all study areas which is potentially influenced by higher rates of harvest (Figures 5, 6, and 7 and Tables 4 and 6) compared to females. For example, 34.6% of the 2005 estimated population of male wolverines was removed by harvest on the Kennady Lake grid. In contrast, females show higher rates of apparent survival, lower rates of movement and immigration into grid area. Female populations appear to be more stable compared to male populations, however, low precision of estimates compromise definitive estimates of trend.

Differences in demography between sexes have implications in terms of optimal monitoring strategies. Sex-specific estimates of population size, trend, and demographic rates give a much better picture of the actual status of the population compared to pooled estimates. However, power analyses suggest that a higher sample size of wolverines is needed to obtain sex-specific estimates of trend (Table 10). For example, power analyses suggest that initial population sizes above 40 are needed to have adequate power to detect a 5% annual decline in population size in 10 years of monitoring. This result suggests that a multiple study area approach is needed to obtain sex-specific estimates given that population sizes on all grids (except Daring Lake) is less than 40 wolverines.

The actual fidelity/apparent survival of male wolverines is also influenced by the size of grid areas (Figure 8). This result is biologically reasonable in that fidelity of wolverines should increase as grid area increases. However, this result may also be a result of the larger number of male wolverines removed from the Kennady Lake grid and other smaller grids confounding the affect of grid size on apparent survival. This result also does not necessarily explain the decline in male wolverine populations given that the number of immigrant wolverines should approximately equal the number of emigrant wolverines to any area unless the area is a mortality sink. Pradel model estimates suggest that rates of addition (i.e. births/immigration) is higher for males, but is less influenced by grid size. A model with grid area as a covariate for rates of additions was partially supported by the data, however, a null model with no grid area covariate displayed higher support suggesting this relationship is weak (Table 5).

One potential issue with the analysis was the change in study area configuration for the Ekati grid in 2006. The Pradel model assumes that the study area does not change otherwise estimates of trend might reflect a shift in area sampled (and subsequent population size) rather than the actual trend on the study area. The degree of change in study area configuration and size was minimal so it is likely the effect on estimates of λ was not large. However, it is strongly suggested that monitoring methodologies be standardized each year for each area to avoid this extra source of variation.

The results of demographic analysis are challenged by only 2 years of monitoring data. This is the minimal number of data to determine a trend. At least 3 to 4 surveys are needed to verify some of the relationships suggested by the Pradel model demographic analysis. For example, analysis of 3 years from Daring Lake suggest that females in this area are decreasing in this area whereas estimates from the 2 years in this analysis make this trend less certain. Power analysis does suggest that sampling can be reduced to biannual effort after 2 or 4 years with minimal loss of power (Table 10). However, more sessions will enhance the resolution to further verify some of the demographic relationships suggested by this 2 year analysis.

5.2. Population estimation

Estimation of population size for study areas was successful in that capture probabilities were above 0.5 therefore ensuring robust population estimates from the Lincoln-Peterson estimator and 2-session MARK estimators. Behavioural response was not detected in the data, however, this is likely due to the low number of sessions (2) and subsequent lower power to detect this form of capture probability variation. However, capture probability variation such as heterogeneity and behavioural response have most influence on estimates when capture probabilities are lower, and therefore, the intensive sampling strategy employed mitigates these issues and the need to use more intensive mark-recapture models to estimate abundance (Otis et al. 1978, Pollock et al. 1990, Williams et al. 2002, Mulders et al. 2007). Given this, there is less need with the 3x3 km cell size design to conduct more than 2 sessions that are needed to model heterogeneity and other forms of capture probability variation (Mulders et al. 2007). Sample sizes were low for some areas, however, in most cases precision of estimates was high (CV's of less than 10%) which was mainly due to high capture probabilities (Table 6). Estimates in this case correspond to the population of wolverine in and around the sampling area. These estimates are probably the best representation of the number of wolverines one might encounter in the study area if traversed during the time period that sampling took place. However, it is difficult to compare study areas given that the study areas were different size. For comparison of study areas, density estimates are desirable.

5.3. Density

Estimates from program DENSITY demonstrate that a reasonable proportion of wolverines that area found in sampling areas spend some degree of time off DNA grids. The difference between the average number of wolverines on the grid at any one time and superpopulation estimates of wolverines in and around the grid area and ranged from 24 to 74% (Table 8). Males had a greater tendency to spend more time off the grid compared to females.

It is important to note that individuals that are captured in multiple study areas will not bias density estimates. This is because DENSITY does not assume that any of the wolverines captured are permanent residents of the sampling grid. It basically simulates the fact that some wolverines may live partially off the grid (and on other grids) while sampling is occurring. Program DENSITY also assumes that wolverines have circular home range areas and that movements and distribution of wolverines across grid borders or within grid areas is similar. It is possible to add in a habitat mask that simulates areas that are not traversed during sampling. In addition, future versions of DENSITY should allow actual habitat types to be simulated.

Density estimates for Diavik from this study differ from those presented by Golder (2007). Density estimates from Golder (2007) were not corrected for closure violation whereas we used DENSITY to model and directly estimate density. This resulted in density estimates of Golder (2007) being 2.3 to 2.4 times higher than those reported in Table 8. We suggest that correction for closure violation is essential in estimation of density. Otherwise, density estimates from smaller study areas will be positively biased.

5.4. Trend monitoring

5.4.1. The need for multiple study areas

A fundamental objective of monitoring efforts is to determine potential changes in wolverine populations due to activity in mine areas and to separate perceived changes due to other factors such as wolverine harvest and natural changes in wolverine population size. One of the main advantages to the monitoring of Daring Lake and mine areas is that it allows separation of overall population trend within the larger-scale area with regional trends at each of the mine sites. For example, consider if only the results from an individual mine area were available. In that case it might be concluded that the population of wolverines is declining around the mine areas and it might be concluded this is due to mine activity. However, estimates from the Daring Lake study site area, and other mine sites suggests a larger-scale trend, which is potentially due to harvest or other natural factors. In addition to wolverine mortalities caused by resident and sport hunters on the central barrens, between 1998-2005, an estimated 30 wolverines have been either killed or relocated from the Lac de Gras region in connection with mining related activities. These results exemplify the need for a larger-scale multi-study area approach to allow robust estimates of trend and inference of factors influencing trend across a range of scales.

Results from the Pradel model robust design were somewhat limited due to 2 years of monitoring data. However, even with 2 years of data potential differences in demography between sexes and relationships between scale (grid size) and male demography were suggested. Future analysis could potentially reveal more exact reasons for differences between areas in terms of demography. Key to this approach is the joint modeling of all data sets. Besides enhancing estimate precision, this approach allows an estimate of spatial variation in demographic trends as well as an opportunity to test hypothesis about causes of demographic differences between study areas (through the use of covariates). Examples of covariates that might be used to explain differences in demography between study areas are given in Table 9. Wolverine mortalities were used in this year’s analysis with minimal support from the data. However, this was potentially due to low resolution from only 2 years of data.

Table 11: Possible covariates for wolverine trend monitoring

Apparent survival (ϕ)	Rates of addition (f)	Capture probability (p)
Wolverine mortalities	Caribou/prey availability	Weather during sampling
Wolverine removals	Mine activity	
Mine activity	Winter severity	

Power analyses are a very simplified method to determine optimal sample sizes for monitoring in that they reduce the adequacy of monitoring into potential outcomes of a single hypothesis test. A modern trend monitoring project should be able to do more than detect change in population size. It should be able to also associate potential factors associated with the estimated trends (Boulanger et al. 2004). Given this, power analyses should mainly be used to compare relative efficiency of sampling designs with the understanding that the ultimate objective of monitoring goes beyond simply detecting trends in population size.

The Pradel model is only one of many mark-recapture models that can be used to estimate and explore population demography of wolverines. If suitable numbers of wolverine mortalities are genotyped in study areas then it is possible to use a joint DNA hair snag captures and dead recoveries model (Burnham et al. 1987). This model provides enhanced estimates of survival since true mortalities are included in the input data set. Another model that has potential use is the multi-strata model (Hestbeck 1982, Brownie et al. 1993). For this model, the study area where a wolverine is captured is included in the data set. If wolverines are captured at multiple study areas then it is possible to use this model to estimate movement rates between areas. In addition, this model can incorporate both DNA hair snag captures and dead recoveries. It is strongly suggested that DNA samples are taken from all wolverines killed or translocated from study areas to allow the potential use of these models in the future.

Power analyses suggest that at least bi-annual sampling after 2 to 4 years of annual sampling is needed to ensure reasonable levels of power. Power analyses also suggest that initial population sizes of at least 40 wolverines are needed to ensure adequate power to detect an annual 5% decline. This result contrasts to the recommendation of Golder (2007) that tri-annual sampling is adequate to detect a very small decline (0.67% per year) in abundance for the Diavik study area. The estimate of greater power from Golder (2007) is probably due to how their power analysis was conducted. Golder (2007) used program MONITOR (Gibbs 1995) for power analyses. Program MONITOR is designed for count-based trend monitoring projects as opposed to mark-recapture based monitoring projects. Given this, it is not possible to specify the appropriate variance model for the influence of population size on variance given that the inherent relationship between variance and abundance is different for mark-recapture and count based analyses (Gerrodette 1987). In addition, count-based methods, as simulated in program MONITOR, assume that yearly capture probabilities of wolverines are constant therefore not simulating variance in capture probability which will lead to optimistic power estimates. In contrast, simulations in MARK simulate capture probability variation that will produce less optimistic but more reliable estimates of power. Given this, we suggest that our power analysis provides a more realistic estimate of the true power of mark-recapture methods.

5.5. Comparison to track-count methods

The monitoring of temporal trends, density and abundance provides a more sensitive and biologically meaningful method to assess wolverine response to mine development than other methods such as track counts that attempt to estimate wolverine distribution relative to mine sites. The reason for this is that highly spatial mobile animals probably do not respond to mine sites in a “zone of influence” scale. For example, analyses in DENSITY (Figures 10 and 11) suggest a male wolverine can traverse the entire survey area in relatively short periods of time and therefore the actual scale of movements prevents detection of smaller scale changes in distributions relative to mine sites especially since male and female tracks cannot be differentiated. Golder (2007) suggests that track transects might detect “avoidance” or “attraction” of wolverines to mine sites as determined by decreasing probability of occurrences as a function of distance to mine sites. However, the “avoidance” effect could also be generated by increased mortalities near mine sites creating a temporarily lower density of wolverines near the mine site. In that case it might be concluded that wolverines are avoiding or not attracted to mines when actually mortality or removals is creating a “sink” area around mine sites. DNA-based methods allow estimation of sex-specific apparent survival and the relative contribution of apparent survival to overall population trend. It is through monitoring of these two parameters that trends in mortality and their contribution to trend can be monitored effectively.

6. Recommendations

The following recommendations are made in point form.

1. The analyses conducted in this paper suggest distinct spatial patterns, demography and trends between sexes of wolverines. We suggest that sex-specific analyses are conducted on future data to allow more firm inference about the true biological status of populations. This requires more intensive sampling than pooled estimates but also provides much more meaningful results.

2. More years of data are needed to verify demographic relationships and estimates of trend of wolverine. We suggest that sampling should be conducted for at least 2 more annual sessions to verify the potential sharp decline in males suggested in the analysis. After 2 more annual surveys it should be possible to reduce effort to biannual surveying. The fact that surveys were not conducted in 2007 can be accounted for in future analyses.

3. Genotyping of carcass samples from hunters and trappers provides valuable inference on source of mortality and potential reasons for observed demography. We suggest that the program of genotyping carcasses or any translocated individuals be conducted throughout the study area. In the future, analysis that more directly incorporate mortality data should be possible.

4. The same design methodologies (bait post layout, session length, timing of sampling, number of sessions) as in 2005 and 2006 should be used for each of the project areas in future surveys. Changes in methodology will make the modeling of trend and demography problematic in that changes in trend will be confounded with the effects of change in methodology.

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The collection of wolverine genetic samples in 2005 and 2006 involved many individuals working for BHPBilliton, Diavik Diamond Inc., DeBeers Canada, and the GNWT Department of Environment and Natural Resources. Specifically, BHPBilliton personnel included Brent Murphy, Elizabeth Miller, Jorgen Bolt, Patrick Kramers, David Abernethy, Maurice Boucher, Ross Lehune, Charles Klengenberg and Scotty McLeod. Diavik Diamonds Inc. personnel included Scott Wytrychowski, Scott Morrison, Colleen English, Seth Bohnet, Karl Cox, Ray Eskelson, George Taptuna, Bobby Algona, and Peter Katiak. Individuals working for DeBeers Canada and/or AMEC Earth & Environmental included Robin Johnstone, Raymond Marlowe, Joseph Catholique, Derek Michel, Chris Godwin-Sheppard, Eric Hamelin, James Clark, and Janet Bauman. GNWT ENR employees included Ray Case, Rob Gau, Dean Cluff, Dave Taylor, Paul Mackenzie, James Sangris, Patrick Charlo, Lawrence Goulet, Edward Doctor, Nap Mackenzie, Shalene deWynter, Sunny Ashcroft, Joanne Wilson, Joel Gowman, Lesley Johnson, Sarah Stevenson, Jean-Francois Dufour, Credence Wood, John Lee, Cindy Taylor, Steven Matthews and Adrian D'Hont. Many ENR staff at the North Slave regional office assisted, primarily with the collection of carcasses, including: Shelly Acton, Irene LeMouel, Raymond Bourget, Janice Ziemann, Patricia Handley, Albert Bourque and Danny Beaulieu. Golder (2007) collected track count data and conducted preliminary analyses for the Diavik study area.

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