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Survival of an Exploited Grey Wolf Population in the Northern Rocky Mountains: Density Dependence and Licensed Hunting

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A thesis submitted in partial fulfilment of the requirements for
the degree of Master of Science of Imperial College London and
Diploma of Imperial College London

September 2011

Abstract

Large carnivore extinction has occurred throughout history as a consequence of human expansion. Reintroductions and federal protection through the 20th century have seen a rise in carnivore populations. Key to their success is detailed knowledge of demographic parameters and habitat suitability. Presented here is a mark-recapture-recovery analysis of the Northern Rocky Mountain Grey Wolves (*Canis lupus*) in Idaho, Yellowstone National Park and Wyoming, accompanied by an analysis of the effect of anthropogenic mortality on survival rates. I found that in two of the original recovery areas survival rates have decreased and that population viability may be at risk with licensed hunting now occurring in Idaho and low recovery probabilities suggesting high rates of illegal take. Pooled survival rates in Yellowstone National Park decreased from 0.737 (0.672, 0.795; 95% CI) to 0.614 (0.536, 0.689) and from 0.776 (0.726, 0.820) to 0.518 (0.464, 0.573) in Idaho during the periods 2005-2007 and 2008-2010 suggesting carrying capacity has been reached in YNP and a the population is on the verge of decline in Idaho. This could have direct effects on the sustainability of the population in Montana with the effect of anthropogenic mortality found to be partially compensatory in Yellowstone National park but additive outside, a cause for concern in light of the reintroduction of licensed hunting in Idaho and Montana.

Contents

1. INTRODUCTION

As human population increases, large carnivore populations decline (Duncan, 2002,Woodroffe, 2000). This is because people dislike living among animals that can kill them, their pets, their livestock and large carnivores are often revered in myths and folklore (Roskaft, 2003, Packer, 2011). Consequently, large carnivores have been persecuted throughout human history, with mankind implicated in multiple global and local carnivore extinctions (Beck, 1996, Choquenot, 1998, Paddle, 2002). Carnivores often have large territories and low densities which result in their populations being difficult to study and being extremely vulnerable to fluctuations in their numbers caused by habitat removal, increased barriers to dispersal and anthropogenic mortality (Woodroffe, 2000, Gittleman, 2001, Cardillo, 2004). As carnivores are extirpated from regions, unpredictable and undesirable trophic cascades can occur which impact on entire ecosystems, changing species composition and biodiversity of habitats (Schmitz, 2000, Berger, 2001, Miller et al., 2001). Conservation is far from simple for species which are either loved or hated, but never somewhere in between (Cardillo, 2004) and with the exponential increases in global population, human-carnivore conflict is guaranteed to increase worldwide (Johnson, 2006, Michalski, 2006).

As conservationists are increasingly aware of the impacts of altering natural ecosystems, there is increasing interest in restoring large carnivore populations where they have previously been extirpated, and preserving current populations, while mitigating human-carnivore conflicts (Williams, 2002). The need for sustainable conservation and reintroduction plans that benefit humans, ecosystems and are viable at high human densities, have never been more pressing (Clark, 1996, Berger, 1999, Linnell, 2001, Treves, 2011).

Biological and non-biological factors play a key role in reintroductions; with detailed knowledge of demographic and fiscal parameters key to their success (Miller, 1999). It is therefore paramount to gain as much insight as possible from prior reintroductions on demographic parameters, habitat suitability and the effect of anthropogenic mortality, either through control actions or licensed

hunting to manipulate survival rates or carrying capacity (Hayward, 2007). Mark-Recapture-Recovery (MRR) methods have provided key insights into survival rates and population abundances of large carnivores (Karanth, 2006, Cubaynes, 2010).

MRR analysis allows flexibility in modelling, analysis of multiple data sets and permits model selection through various selection criterion (Lebreton, 1992). The rise in popularity of MRR models in Ecology over the past two decades highlights the important impact they have had on this discipline. Their utility in explaining the drivers of population fluctuations over time, both environmental and demographic, has made them key tools for management and conservation practices (Cam, 2004, Johnson, 2004, King, 2006)

The grey wolf (*Canis lupus*) population in the Northern Rocky Mountains (NRM) and especially inside Yellowstone National Park provides a unique view into the effect top order predators have on an ecosystem, from which they were removed less than 100 years before (Hayward, 2009). Analysis of survival rates, recapture and recovery probabilities contribute to predictions of population viability (Sollmann, 2010), total population size and the rate of illegal harvest, each of considerable importance due to the recent removal of grey wolves from the endangered species list in Idaho and Montana. The NRM grey wolves invoke strong opinions biologically, socially and politically. With reintroductions and conservations efforts occurring globally (Boitani, 2000, Nilsen, 2007), the analysis presented here gains vital insight into the speed with which reintroduced species can be removed from protective status and the impact of empowering local communities through licensed hunting has on population viability.

The initial growth rates in Yellowstone National Park (YNP) match those seen in other areas (19 % in Sweden and Finland (Wabakken, 2001, Hayward, 2009)) demonstrating that the NRM population is a model example for future reintroduction plans. Studies on the Northern Rocky Mountains wolves (Smith et al., 2010, Murray et al., 2010) have focussed on the expanding population and this is the first to look at the stabilising population inside of YNP. Population

abundance estimates suggest that this is the case and that populations are continuing to expand outside in Idaho and Wyoming (U.S. Fish and Wildlife Service et al.). Dispersal among grey wolves has been known to exceed 800km such that larger than current population densities may be required to see density dependence (Mech, 1995, Boyd., 1999) although the effect of legal and illegal hunting may reduce this natural capacity.

Without reintroductions, fertility control (Garrott, 1995) and/or large scale culls are required, A method preferred by those with a vested interest in big game hunting. However, these methods are often expensive, ineffective and top predators, such as grey wolves, have been shown to prey on the weak, injured or elderly leaving the prime individuals to survive and encouraging prey population persistence (Stahler, 2006). This is in stark contrast to hunting tactics which have no selectivity and why large scale culls can result in unpredictable effects on population size through pack disruption (Feingold, 1996) and even, in principle, increase population size (Kokko, 2001). Whether the hunting season in 2009 reduced survival in 2009, or whether delayed impacts were seen in 2010 is investigated here.

Alienating local populations from management plans can result in people taking matters into their own hands, often resulting in large scale carnivore persecution, especially when there is a large investment in game or livestock ranching in the surrounding area (Villafuerte, 1998, Graham, 2005). From 1984 to 2004, almost 80% of total mortality was anthropogenic (Murray, 2010). Previous studies on the NRM wolves have suggested that anthropogenic mortality is additive and in some cases super-additive (Creel, 2010) whereas others suggest that it is partially compensatory (Murray, 2010).

Creel and Rotella used multiple data sets to arrive at the conclusion that off-take may be super-additive, however they failed to incorporate the amount of unreported mortality thus underestimating total mortality. Lebreton presents an excellent review of statistical models for exploited populations (Lebreton, 2005) and highlights the significance of independent estimates of total mortality and total population size and I present the effect of omitting recovery probabilities

and the bias, if any, in results obtained from this. Understanding whether human off take is compensatory or additive, and to what extent, will determine the limits of licensed hunting necessary to maintain a stable population (Marboutin et al., 2003). The debate on the level of compensation has not aided wolf managers in the NRM and I aim to resolve this issue.

Analysis of dead recoveries is essential, not only for estimating total mortality and whether off-take is additive or compensatory, but in understanding the local tolerance of large carnivores. Studies usually focus on interviewing livestock ranchers about their attitudes towards large carnivores, although this do not always reflect their actions (St John, 2011). Here I analyse their actions through recovery probabilities, with low recovery probabilities a sign of high rates of illegal take, reflecting poor attitudes towards wolves (Kaczensky, 2011). With licensed hunting now occurring in Idaho and Montana there is a risk of populations entering into decline (Person & Russell, 2008). I provide the first analysis of the effect the 2009 hunting season had on survival rate in Idaho and whether recovery probabilities increase. This would represent a decrease in illegal takes through empowering the local community, a perceived benefit expressed by many that comes with licensed hunting (Villafuerte, 1998, Graham, 2005).

Smith *et al.* highlighted the importance of Idaho as a sink in sustaining Montana's wolf population but found survival rates in Idaho, Montana and the Greater Yellowstone Area sufficient to sustain all three populations (Smith et al., 2010). Decreased survival rates in Idaho could cause serious concern for population viability in two of the original recovery areas as YNP itself was deemed too small a population to sufficiently sustain the others through dispersal (Smith et al., 2010). The analysis presented here provides unique insight into the effect of licensed hunting in 2009 as well as the change in survival rates due to increased population densities to test whether the three populations are still sustainable, as well as the viability of the Wyoming population, previously unanalysed.

Eradication of large carnivores has been a consequence of human expansion throughout our history. As biological understanding has broadened the key ecological role top predators play has become ever more apparent. For future reintroductions to succeed, the successes and failures of previous projects must be carefully analysed. Key to this understanding is how demographic parameters and human attitudes can be incorporated into a reliable and sustainable management model plan. Survival rates of both protected and controlled populations where both illegal and legal takes occur, are the basis of such models. Accurately assessing the rate of illegal harvest is a difficult problem to analyse and both of the above are tackled here. The unique depth of data recorded in the NRM in both protected and unprotected areas provides an excellent model population to base future reintroductions. With federal protections and reintroductions occurring elsewhere around the world, both of grey wolves (*C. lupus*) and other controversial apex predators such as lynx's (*L. lynx*) and brown bears (*Ursus arctos)* (Schmidt Posthaus 2002,Wiegand, 2004, Marucco, 2010), similar obstacles will be faced and the analysis presented here will provide answer key questions at the core of their management plans (Haight, 1998, Randi, 1999, Wabakken, 2001,).

2. METHODS

2.1 Study Areas

The Idaho study area consists of three major mountain chains and 2 large rivers. The diverse landscape of sagebrush covered flatlands in the south is contrasted by extreme peaks in the north with elevations varying from 457m to 3,657m. . The US Fish and Wildlife service works in partnership with the Nez Pierce Tribe, who are responsible for wolf management on the Nez Pierce Reservation, and the USDA Wildlife Services, except in 2009 when delisting occurred and wolf management was the responsibility of the Idaho Department for Fish and Game along with the Nez Pierce Tribe.

Wyoming spans 253,346km^2 consisting of large mountain ranges and deep valleys, with altitudes ranging from 945m to 4210m similar to the landscape

found in Idaho. A population of 0.5 million people means it has one of the lowest population densities in the United States. The human population in Idaho is 1.5 million and is also one of the lowest population densities in the USA. Central Idaho is a large area of wilderness encompassing almost 4 million acres. The large Central Idaho Wilderness area means there areas of extremely low population density mixed with areas of moderate density.

Yellowstone National Park (YNP) lies in the states of Idaho, Montana and mostly in Wyoming. It contains 8,983m^2 of land comprising of lakes, canyons, rivers and mountain ranges. The protected status of national parks requires that there is no hunting and in depth scientific research occurs year round. Large elk (*Cervus Canadensis*) and bison (*Bison bison*) populations along with big-horn sheep (*Ovis canadensis*) provide abundant prey for grey wolves (*Canis lupus*).

The Wolf populations are classed as non-essential experimental populations under the endangered species act section 10(j) (Anon., 1973) and are subject to control actions from the US Fish and Wildlife Service, usually due to livestock depredations and occasionally habituation to humans. Individuals of all age classes are collared using both radio-collaring and darting throughout the summer in Idaho and Wyoming and via helicopter darting from October through March in YNP. Both GPS and VHF collars were used that increase signal pulse upon mortality. On-site exams at mortality sites combined with lab necropsies determined causes of death. In YNP individuals were tracked via aircraft every 14 days and up to daily during winter studies where analysis of behaviour and locations of the wolf packs are recorded. Their studies include detailed analyses of hunting behaviour, population genetics, diseases, pack leadership, breeding behaviour and many other covariates (Stahler, 2006, Vonholdt, 2008). Tracking frequencies outside of the park were not given but occurred at greater than one survey per season so that delayed recoveries could be safely ignored.

Successful retrieval of a telemetry signal is counted as a recapture in this study and mortalities are counted upon sighting of an individual or through retrieval of mortality signal transmissions. The depth of the data allows for detailed and accurate analysis of demographic parameters essential for understanding the

roles top order predators play in ecosystems. The analysis of recapture and recovery probabilities enables accurate predictions of total annual mortality and total population size, often greatly underestimated by total reported size (Person & Russell, 2008). This is essential to predict the reintroduced species success and also the impact the 2009 hunting season had on population growth rate.

2.2.1 Statistical Analysis and Modelling

An individual is classified as being released into the study upon initial capture. Difficulties arrive here as individuals could have been collared prior to 2005 and may have emigrated out of the study areas. It is therefore assumed that an individual is not present in the study area until it is either captured for collaring or is recaptured for the first time post 2005, having previously been collared during another study.

Individuals were omitted from the population if they were never recaptured or only recovered dead in this study having been released prior to 2005 as they could not be confirmed as being alive and present in the study areas after 2005. Known collar failures were right censored back to the last known functional time as failure to do this will violate the assumption of homogeneity among individuals. Without a functioning collar recaptures and recoveries can only occur through visual sightings. This restricts their range in comparison to individuals with working collars.

Collaring of Pups occurs from July onwards in Idaho and Wyoming and from December onwards in YNP. This did not permit accurate analysis of pup survival in YNP, as all individuals must be released into the study none could be recorded dead during their first season. Pups could go missing from the population having been collared so pup survival was not guaranteed to be estimated at 1. No information on pup survival during the first season of denning is given in the capture history data as it is not possible to capture individuals while they are in the den. The estimation of pup (0-1 yrs) survival rates in Idaho and Wyoming was restricted to 9 months survival rates.

Mark recapture data provided consisted of annual data divided into four seasons; January through March, April through June, July through September and October through December. Wolves den in April and pups first leave the denning area in October. The denning season is therefore defined as April through September. Capture history data provided consisted of a 1 if an individual was marked or recapture in the time interval, a 0 if the individual was missing and a 2 if it was recovery dead. For example a study conducted over 8 capture events with n time varying and 2 time invariant covariates would be:

$$
\begin{array}{cccccccccc}
0 & 0 & 1 & 1 & 0 & 0 & 1 & 2; & S & C.R \\
Y_{1,0} & Y_{1,1} & Y_{1,3} & Y_{1,4} & Y_{1,5} & Y_{1,6} & Y_{1,7} & Y_{1,8} & & \\
\cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & & \\
\cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & & \\
\cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & & \\
Y_{n,0} & Y_{n,1} & Y_{n,3} & Y_{n,4} & Y_{n,5} & Y_{1,6} & Y_{n,7} & Y_{n,8} & &
\end{array}
$$

The time-varying covariates $Y_{i,j}$ represent covariates such as location and age class. S and C.R are time invariant sex and capture-reason covariates. The covariates are used to define the survival rate, recapture and recovery probability to each individual at each time step. Note that multiple recaptures in a season are ignored; it is only of concern that an individual was recaptured, recovered or missing in a given season.

The mark-recapture-recovery method used is derived using the methodology defined in detail by Catchpole *et al.* (Catchpole, 2000). Define:

$$\varphi_{i,j} = \text{The probability that individual i, alive at time j survives until time } j + 1$$

$$P_{i,j} = \text{The probability individual i is recaptured at time j | it is alive at time j.}$$

$$\lambda_{i,j} = \text{The probability that individual i is recovered in time step j | it died in time step j}$$

Catchpole *et al.* derive the likelihood using individual cohorts and use a separate likelihood function for each covariate. Scarcity of data did not permit analysis of each cohort and their corresponding covariates. Instead individual covariates were pooled together to act similarly to cohorts. Define:

$$w_{i,j} = \begin{cases} 1 & \text{if individual } i \text{ is recapture at time step } j \\ 0 & \text{otherwise} \end{cases}$$

$$z_{i,j} = \begin{cases} 1 & \text{if individual } i \text{ is known to be alive at time step } j \text{ but not recaptured} \\ 0 & \text{otherwise} \end{cases}$$

$$d_{i,j} = \begin{cases} 1 & \text{if individual } i \text{ dies in time step } j \\ 0 & \text{otherwise} \end{cases}$$

$$v_{i,j} = \begin{cases} 1 & \text{if individual } i \text{ is not seen again after time step } j \\ 0 & \text{otherwise} \end{cases}$$

$$r_{i,j} = \begin{cases} 1 & \text{if individual } i \text{ is released in time step } j \\ 0 & \text{otherwise} \end{cases}$$

The likelihood, $L(y|\theta)$, on the set of parameters, θ, and data set y, is defined as:

$$L(\theta|y) = \prod_{i=1}^{n}\prod_{j=1}^{T} \varphi_{i,j}{}^{k_{i,j}} . P_{i,j}{}^{w_{i,j}} . \left(1 - P_{i,j}\right)^{z_{i,j}} . \left(\left(1 - \varphi_{i,j}\right).\lambda_{i,j}\right)^{d_{i,j}} . \prod_{i=1}^{n}\prod_{j=1}^{T} x_{i,j}{}^{v_{i,j}} \ (1)$$

$$k = w + z + r - v$$

$$x_{i,j} = \left(1 - \varphi_{i,j}\right).\left(1 - \lambda_{i,j}\right) + \varphi_{i,j}.\left(1 - P_{i,j+1}\right).\chi_{i,j+1}$$

$$\chi_{i,T} = 1$$

Assumptions of the model:

1. Recapturing occurs instantaneously
2. Individuals are homogeneous with respect to covariates

3. Populations are closed or emigration is small enough to be negligible
4. There are no delayed recoveries. A mortality that occurs in a given season is either reported in that season or never reported at all.

I impose as *a priori* that only continuous covariates may be combined in the model such that, for example, old adults and pup survival cannot be combined. The second *a priori* is that recapture and recovery probabilities will not vary among age classes or sex as the method of recapture does not benefit an individual of a certain type. Recapture and recovery probabilities are free to vary across time periods, annually or seasonally, but again only consecutive time steps are permitted to be combined and if they vary they must vary across all age classes identically.   The final *a priori* is that there will be variation in recapture and recovery probabilities for the covariates of pack-membership and capture reason. Dispersing wolves will leave pack territories where it is easier for them to be tracked and a greater effort may be used to track individuals collared for livestock purposes and recapture and recovery efforts may differ seasonally and annually due to various conditions. I therefore allow recapture and recovery rates to vary across these covariates.

Confidence intervals were calculated using the likelihood ratio test where;

$$\Lambda = -2\log\left(\frac{L(y,\theta^*)}{L(y,\vartheta)}\right)$$

$$\Lambda \sim \chi_1^2$$

Where θ^* is the set of optimal parameters, and θ the alternative set. Using the fact that D follows a χ^2 distribution on 1 degree of freedom, confidence intervals are obtained when the set of parameters, θ, yields a significantly different model fit. A 5% confidence level is used throughout the analysis. Optimisation of the maximum likelihood estimate and likelihood profiling were performed using the statistical programme R.

Table 1. Factor levels tested for each covariate

Covariate	Levels
Age Class	0-1 yrs
	1-2 yrs
	2-6 yrs
	7+ yrs
Annual	2005
	2006
	2007
	2008
	2009
	2010
Capture Reason	Monitoring
	Targeted
*(Idaho, YNP)	
Location	Idaho
	YNP
	Wyoming
Pack Membership	Resident
	Disperser
*(YNP, Wyoming)	
Season	January-March
	April-June
	July-September
	October-December

*() Factor level only

Individuals with missing covariates were omitted from the analysis to permit model selection using the AIC.

$$AIC = -2 \log L + 2.K \qquad (2)$$

$$k = \text{number of parameters in the model}$$

A ΔAIC value of >2 is required for a model to have a significantly better fit. If models do not decrease the AIC value by more than this then the simplest model is taken to agree with parsimony. Johnson and Omland give a review of model selection and the use maximum likelihood estimators in ecology (Johnson, 2004). The sample size here is large enough that it is not necessary

to correct for small sample size (>6000 data points). Individuals with missing covariates for capture reason or pack membership were assumed to be collared for monitoring purposes and to be pack residents respectively as these individuals had a greater probability of being pack members and collared for monitoring purposes. Large sample sizes for pack residents and individuals collared for monitoring purposes in comparison to dispersers and individuals targeted for collaring, ensures no bias will incurred.

The over-dispersion parameter $\hat{c}$ is tested for using likelihood ratio tests between the theoretical fully saturated model and the maximal parameterised model possible.

$$\hat{c} = \frac{\text{residual deviance}}{\text{residual degrees of freedom}} = -2 \frac{\log\left(\frac{L(M_s|y)}{L(M_m|y)}\right)}{D_s - D_m}$$

Where M_s is the fully saturated model on D_s degrees of freedom and M_m is the maximal model on D_m degrees of freedom.

Over-dispersion is usually caused by heterogeneity of individuals. This would be in violation of assumption 2 of the model. If over-dispersion is found then the AIC is replaced by the Quasi Akaikes Information Criterion (QAIC) which divides the log likelihood in (2) by the over-dispersion parameter $\hat{c}$ (Anderson et al., 1994). In the presence of over-dispersion the likelihood estimates over-estimate the lack of fit, so it is necessary to compensate for this.

A comparison with the previous survival study (Smith et al., 2010) where Cox Proportional Hazard Models were used (Andersen, 1982), is presented in Appendix (1). In this study YNP was incorporated into the larger Greater Yellowstone Recovery Area encompassing parts of Idaho, Wyoming (outside of YNP) and southern Montana.

2.2.2 Compensation

Compensation is analysed by comparing the covariance between the proportion of anthropogenic and natural mortality (Lebreton, 2005). The survival rate in

year Y, S_Y, is a function of the probabilities of natural mortality, V_Y, and anthropogenic mortality, K_Y. Such that:

$$S_Y = 1 Su V_Y - K_Y \qquad (3)$$

The correlation between natural mortality and anthropogenic mortality is close to zero and mostly negative under additivity. Assumptions must be made about the reported deaths of unknown causes and unreported deaths. Using the recovery probabilities it is possible to predict total mortality. The recovery probabilities derived in (1) can be applied to estimate the total annual mortality by:

$$M_Y = \sum_{i=1}^{4} \frac{1}{\lambda_i} \cdot (n_i + h_i + u_i)$$

Where M_Y is the total mortality in year Y, n_i is the known amount of natural mortality in season i, h_i is the known amount of anthropogenic mortality and u_i the amount of unexplained mortality in year i. From this we can estimate the amount of unexplained deaths in each location. Attributing the unexplained mortality to both human and natural causes, we can determine sensitivities of the correlation between V_i and K_i. Total population size can be estimated from recapture rates with:

$$N_Y = \frac{1}{1 \prod_{i=1}^{4} \overline{P_i}} \cdot \widehat{N}_Y$$

Where N_Y is the total population size, in year Y, $\widehat{N}_Y$ is the total observed population and P_i the recapture probability in season i derived in (1). Compensation can be calculated seasonally although low seasonal mortality may restrict the analysis of 24 separate recovery rates. It is possible to derive separate survival rates defined in (3) such that compensation can be analysed in each of the three study areas.

3 Results

3.1 Survival Analysis

Results presented here are a combination of seasonal (3 month), 6 month and annual survival rates. All recapture probabilities presented are seasonal probabilities. Recovery probabilities are the probability that a death is reported and are independent of the length of time steps. It is explicitly labelled when the survival rates presented are not annual survival rates.

From 2005-2010 699 individuals were monitored in the three study areas. 613 were included in the analysis (Table 7) of which 295 were male and 318 female. 296 individuals were included in the study from Idaho, 167 in YNP and 166 in Wyoming. 138 were tracked as Pups (0-1 yrs), 312 as yearlings (1-2 yrs), 511 as adults (1-6 yrs) and 115 as old adults (7+ yrs). 62 were known dispersers at some period during the study, although information was only given on pack membership in Yellowstone National Park (YNP) and Wyoming (Table 1). 44 individuals were targeted for collaring, the majority (42) were in Idaho (Table 2). Over-dispersion was found to be small with $\hat{c}$ estimated at 1.02 sufficiently close to 1 that the AIC was used for model selection.

100 individuals were lost out of the population during the study in Idaho, 48 in YNP and 30 in Wyoming. 30 individuals were right censored in Wyoming, 6 due to collars being chewed off by other wolves, 5 due to collar malfunction and 19 were GPS collars designed to be dropped (table 6). Information on tag loss was only provided in Wyoming.

The number of radio-collared individuals doubled in Wyoming during the study, peaked in 2009 in Idaho and decreased steadily each year over the duration of the study in YNP (table 6). 106 individuals survived until the end of the study. 36 individuals died of anthropogenic causes in Idaho, 5 in YNP and 36 in Wyoming. 5 died of natural causes in Idaho, 49 in YNP and 13 in Wyoming (table 5).

Table 2. Factor levels for survival rates, recapture and recovery probabilities included in the best model in the three study areas. Each row represents inclusion of an additional factor level.

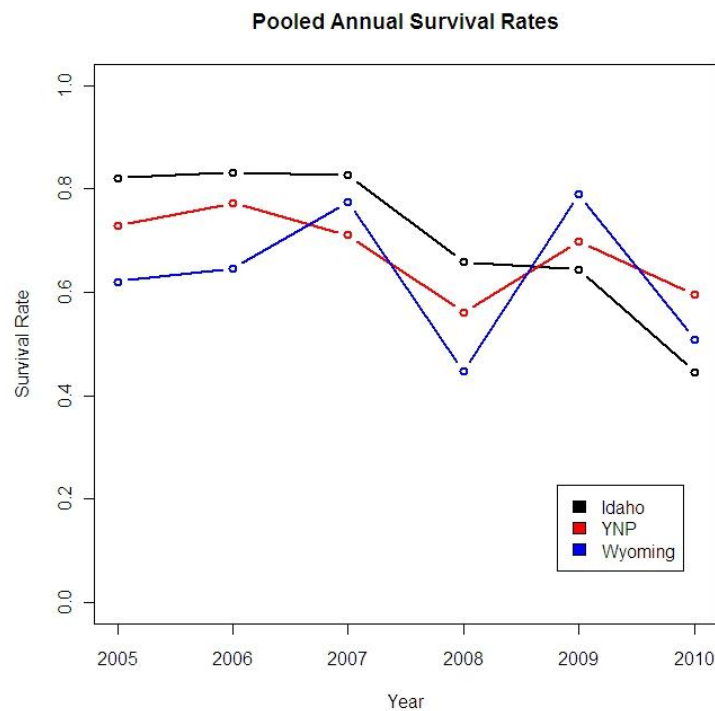|	Factor Levels	*AIC*	Δ*AIC*
YNP			
Survival rate	Pooled	964.853	0
	Pack Residents, Dispersers	956.084	-8.768
	Residents (1-6, 7+ yrs)	948.643	-16.210
Recovery Probability	Jan-March, April-Sept, Oct-Dec *(Residents)	941.126	--24.177
Idaho			
Survival Rate	Pooled	3294.943	
	Monitoring, Targeted	3294.223	-0.72
	Pups, 1+ yrs *(Monitoring)	3292.844	-2.11
	2005-2007 , 2008-2010 *(1+ yrs Monitoring) *(Targeted)	3252.821	--42.122
	Oct-March, April-Sept *(Monitoring) *(2008-2010) *(1+ yrs)	3244.569	-50.374
Recapture Probability	Monitoring, Targeted	3241.443	-53.500
	2005, 2006, 2007-2009, 2010 *(Monitoring)	3225.213	-69.730
Recovery Probability	Monitoring, Targeted	3219.936	-75.007
	Jan-March, April-June, July-Sept, Oct-Dec *(Monitoring)	3207.484	-87.459
Wyoming **Survival Rate**	Pooled	1408.191	
	Pups, Yearlings, Adults, Old Adults	1392.552	-15.640
	Male, Female *(Adults)	1392.623	-15.569
	Jan-March, April-Sept, Oct-Dec *(Male)	1389.028	-19.028
	Jan-June, July-Sept, Oct-Dec *(Female)	1385.855	-22.337
Recapture Probability	2005-2007, 2008, 2009, 2010	1363.17	-45.021

*() factor level only

Figure 1. Annual survival rates in the 3 study areas from 2005-2010. All seasons in a given year were pooled together to analyse survival rates annually.

Survival rates, recapture and recovery probabilities across the three study areas were significantly different $(\Delta \, \text{AIC} = -289.242)$, with survival in Idaho and YNP significantly decreasing from the period of 2005-2007 and 2008-2010 (figure 1). No temporal variation in survival rates improved model fit in Wyoming. Pooled survival across all covariates was highest in YNP at 0.671 (0.633, 0.730, 95% CI; n= 63 deaths) with survival rate in Idaho of 0.645 (0.607, 0.682; n=145) and 0.629 (0.869, 0.910; n=75) in Wyoming.

Variation in survival rates across age classes improved model fit in all three study areas (table 2), with pups having significantly higher survival rates in Wyoming (figure 5) than older individuals. Pup survival was higher in Wyoming than in Idaho (figure 3) as only one pup mortality was reported in Wyoming which was censored due to the mortality occurring during the season of release giving 9 month pup survival in Wyoming of 1 (0.852,1; n=0). Similarly only 1 pup went missing in YNP giving 3 month pup survival estimate of 1 (0.957, 1; 0). 9 month pup survival in Idaho was estimated at 0.718 (0.526, 0.867; n=5) which

would extend to annual survival of 0.643 if it is assumed that survival in the den is equal to survival during the other seasons. This would give pup survival in a similar range to that of yearlings and adults in Idaho, in contrast to that found in Wyoming. No variation was found in individuals of age greater than 1 year in Idaho, although significant differences were found between those collared for monitoring purposes and those targeted for collaring in survival rates (figure 3), recapture and recovery probabilities.

Decomposing survival rates into individuals targeted for collaring and those collared for monitoring purposes only improved model fit when recapture and recovery rates were divided similarly. Fixing recapture and recovery rates between the two forced the variation in recapture and recovery rates onto survival estimates. Similarly dividing survival rates into adult males and females only significantly improved model fit once they were subdivided into seasons (figure 2). Information was not provided on the capture reason in Wyoming and only two individuals were targeted for collaring in YNP which did not enable analysis of this covariate (table 1).

Survival rates in Wyoming decreased as individuals progressed through age classes (figure 4) in contrast to Idaho where no significant differences were found except for pups and in YNP where significant differences were found between yearlings and adults.

Adult and old adult survival rates decreased from the period 2005-2007 to 2008-2010 in YNP with old adult survival always lower (figure 3). Information was provided in YNP and Wyoming on pack membership (table 1) and dispersing wolves were found to have significantly lower survival rates in YNP (figure 3) although no significant variation was found in Wyoming.

No significant variation was found between sexes in Idaho or YNP but variation was found between adult males and females in Wyoming. This difference was found to occur during the denning season (April-September) where male survival rates decreases and female survival increased (figure 2). Variation in survival between the denning and non-denning seasons was also found in

Idaho in the period from 2008-2010, where survival rates decreased outside of the denning season (figure 2).
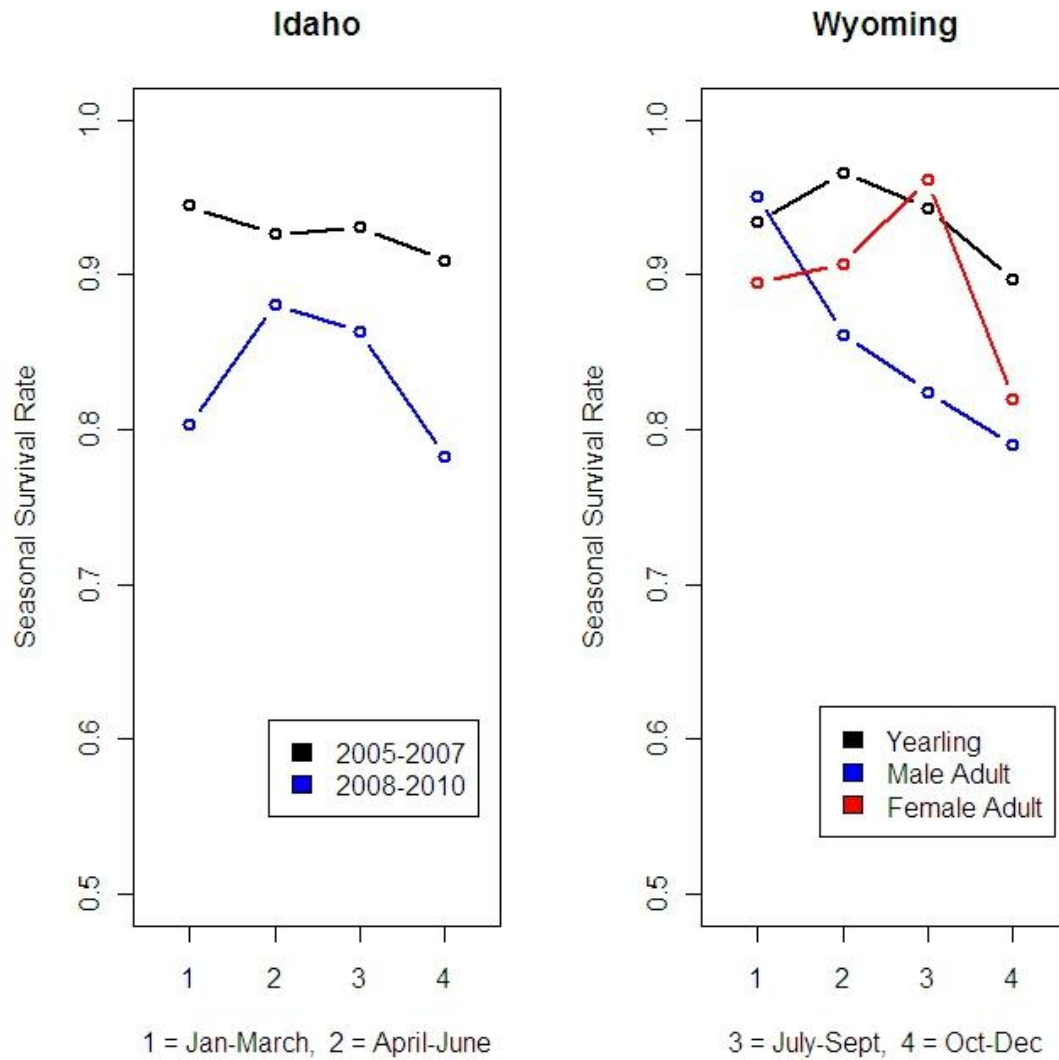

Figure 2. Seasonal survival rates in Idaho (left) and Wyoming (right). Similar seasons in each year were pooled together and analysed as one individual time step.
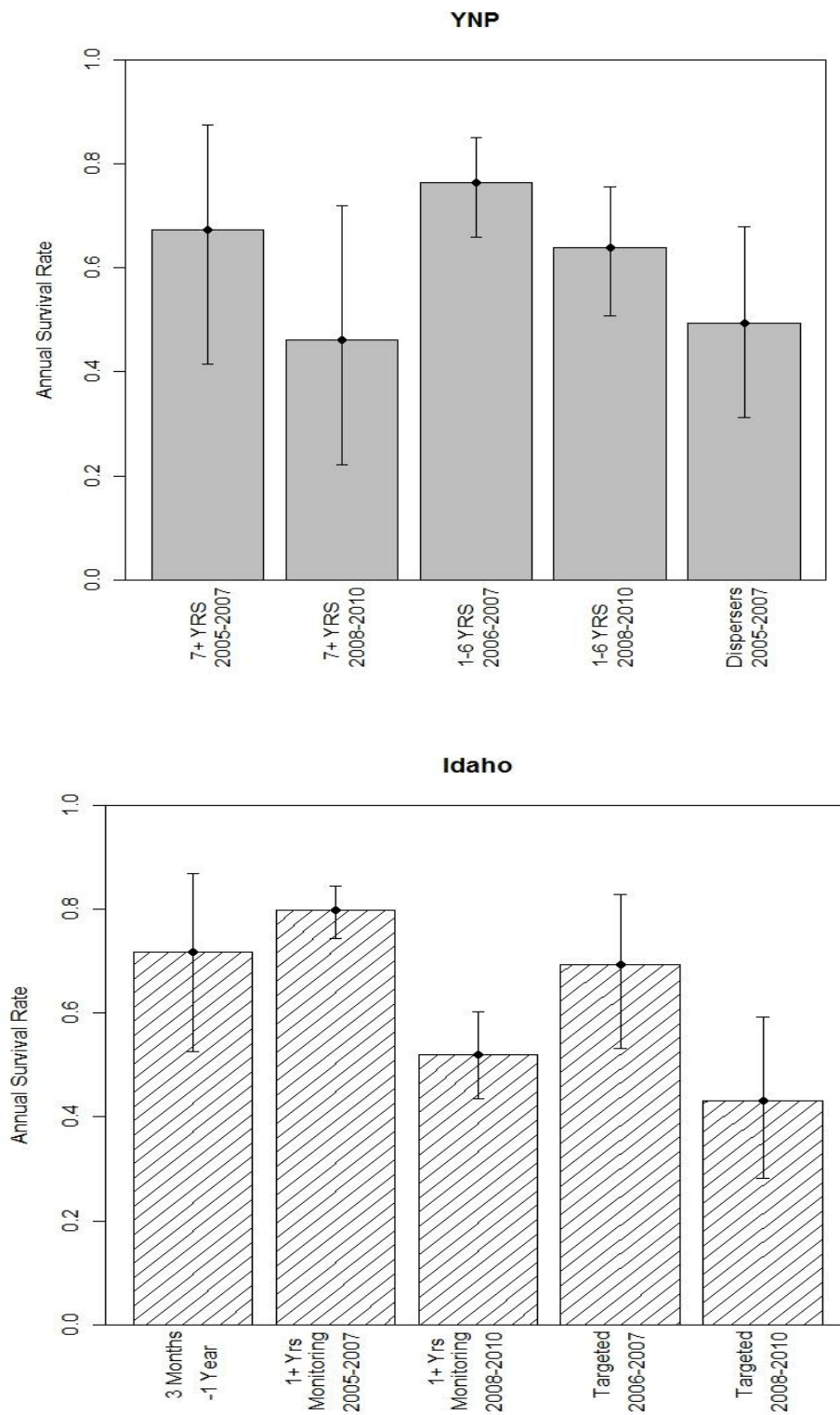
Figure 3. Annual survival rates of different age classes, capture reasons and pack membership in YNP (top) and Idaho (bottom). 3 month -1 year old survival rates given are 9 month survival rates.
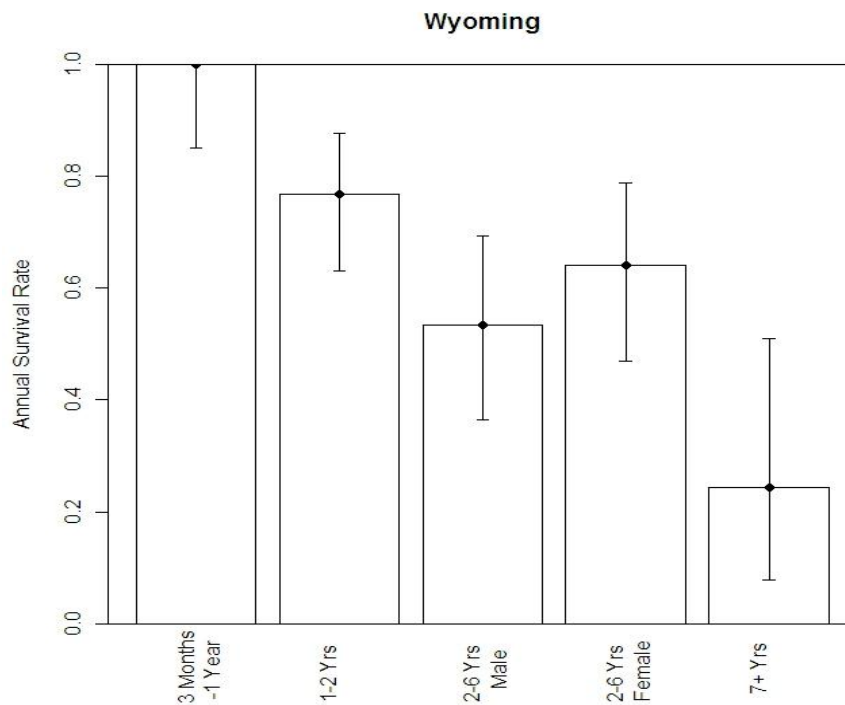
Figure 4. Annual survival rates of different age classes and sex in Wyoming. 3 month -1 year old survival rates are 9 month survival rates.

Recapture probabilities were high in YNP (>.98) every season and significant differences were found in recovery probabilities for pack residents. From January through March recovery probability was 0.362 (0.185, 0.571), for April through September (the denning season) it was 0.587 (0.460, 0.707) and from September through December it was 0.717 (0.534, 0.862) (figure 5). Recovery rate for dispersers was 0.787 (0.536, 0.943). Scarcity of data did not permit varying recovery rates separately over seasons for dispersers.

Recapture and recovery probabilities varied significantly for individuals collared for monitoring purposes in Idaho with individuals targeted for collaring having recapture probability 0.741 (0.708, 0.953) and recovery probability 0.860 (0.672, 0.805). Recovery probability varied seasonally in Idaho for individuals collared for monitoring purposes (figure 5) with recovery probability extremely high in during April-June. It was not possible to test this variation for individuals targeted for collaring due to data lack of data. Recapture probabilities varied annually in Idaho although no significant differences were found from 2007-

2009. Varying recovery probabilities in Wyoming did not improve model fit and was estimated at 0.745 (0.652, 0.826). Recapture probabilities varied from 2008-2010 but no significant differences were found from 2005-2007 in Wyoming (figure 5). Overall recovery probabilities were lowest in YNP at 0.565 (0.471, 0.655), highest in Wyoming 0.745 (0.652, 0.836) and was 0.652 (0.499, 0.776) in Idaho.
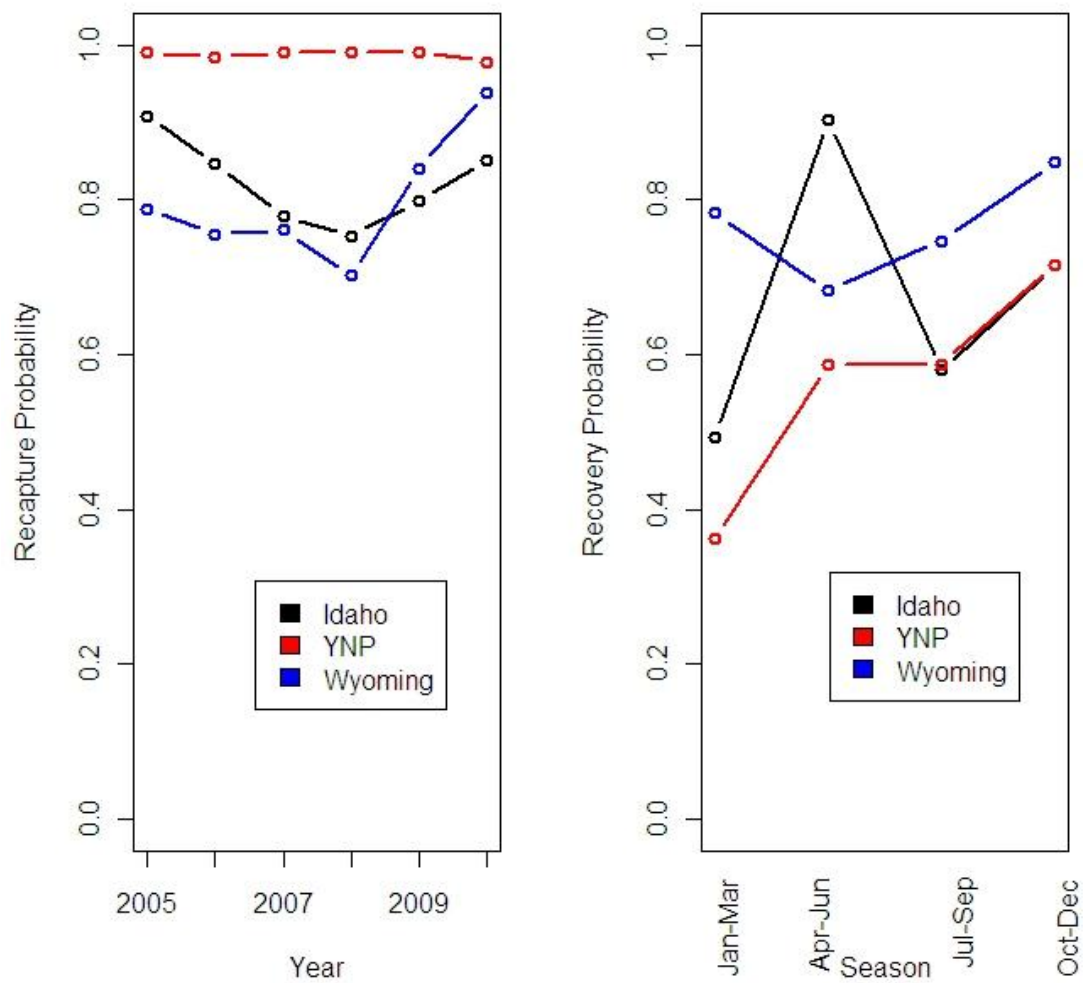

Figure 5. Recapture (left) and recovery probabilities (right) in the 3 study areas.

3.2 Compensation Vs Additive

Table 5. Estimates of total mortality M_i and total population size, N_i from known anthropogenic, h_i and natural, n_i mortality in the 3 study areas.

	YNP				IDAHO				WYOMING			
	M_i	N_i	h_i	n_i	M_i	N_i	h_i	n_i	M_i	N_i	h_i	n_i
2005	26.6	72.0	0	13	15.1	94.0	12	0	10.8	32.1	4	2
2006	10.6	69.0	1	5	21.8	119.0	10	2	14.7	46.2	6	1
2007	14.2	64.0	1	4	22.0	134.3	10	1	12.1	54.2	5	1
2008	33.7	64.0	1	17	57.2	138.3	10	2	29.5	58.6	11	4
2009	15.9	51.0	2	7	45.0	136.3	23	1	9.4	54.0	3	0
2010	5.3	40.0	0	3	47.9	97.2	24	1	24.1	65.0	7	5

Compensation was calculated both prior to and post adjusting population sizes and total mortality. High recapture probabilities resulted in small adjustments of population size such that the rate of compensation was dominated by the adjustment in total mortality. Underestimation of total mortality resulted in a bias towards additivity. The sensitivities of compensation in relation to the cause of unknown mortalities are shown in figure 6. A correlation close to zero shows that anthropogenic mortality is additive.

In Wyoming anthropogenic mortality was always mostly compensatory irrespective of the percentage of unknown mortality that was of anthropogenic causes. Anthropogenic mortality was deemed to be almost completely compensatory in YNP until a threshold level, where most of the unknown mortality was attributed to natural causes (~75%), after which it became partially compensatory. Anthropogenic mortality was partially compensatory under most scenarios in Idaho with a threshold around 10% of unknown mortality being of natural causes, where anthropogenic mortality was additive.
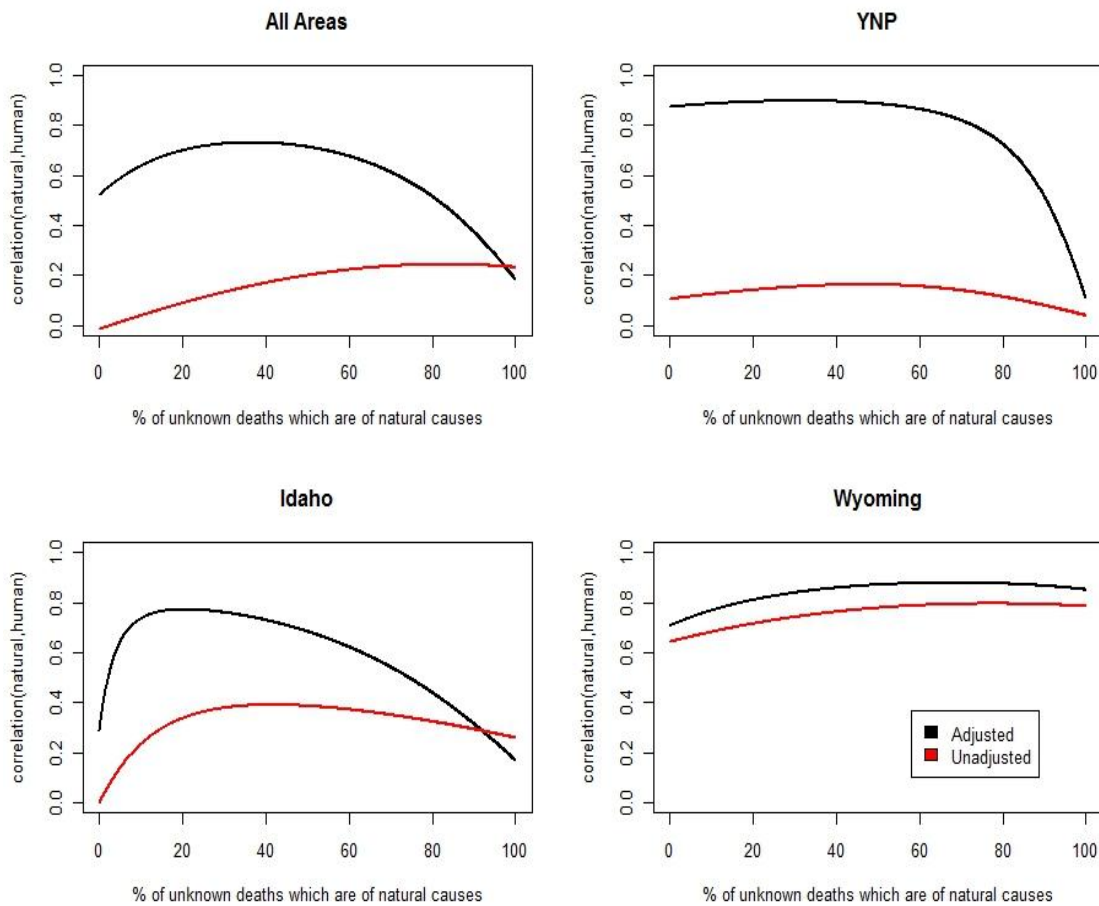
Figure 6. Correlation between human and natural mortality for adjusted and unadjusted population size and total mortality.

4. Discussion

4.1 Analysis

The continued persistence of grey wolves will rely on sustainable management strategies at both state and federal level (Linnell, 2001). These require accurate estimates of survival and illegal harvest rates, the effect of off-take; whether it is compensatory or additive, and accurate estimates of population size. Each are addressed here and with reintroductions, federal protections and management of large carnivores, especially wolves, occurring globally (Cubaynes, 2010), the analysis here provides useful insight which will aid in their future success.

Previous analyses in the Northern Rocky Mountains (NRM) (Smith et al., 2010) showed significant differences in pup survival rates with survival in Idaho estimated at 0.90 and at 0.76 in YNP. The survival rate in Idaho has decreased to levels previously seen in YNP and survival rate in Wyoming of pups was 1, given that there were no reported pup mortalities included in the study. This evidence supports the claim that light density dependence may be occurring in Idaho as it reaches densities previously achieved in YNP.

The previous analysis found no significant difference in survival rates of individuals aged 1+ yrs. I found this to be true in Idaho but found a significant difference in old adult (7+ yrs) survival in YNP and Wyoming. The similarity in Idaho suggests that this difference was not missed in the previous analysis but is due to new environmental pressures acting in YNP most likely due to carrying capacities being reached causing increased intra-specific competition for food (Hassell, 1975) and territories. Survival rates prior to 2007 did not differ from those found previously, suggesting that density dependence or external forces that were not present prior to 2008 are now acting. This was noted in 2008 when survival rates were at their lowest (figure 7) in YNP. An increase in survival the following year suggests compensation, another sign of density dependence.

The low survival rate of old adults in Wyoming is unlikely due to density dependence, rather due to anthropogenic pressures on its population. High anthropogenic mortality (table 5) may prevent individuals from reaching old age and force greater intra-specific competition into the population.

The introduction of licensed hunting in 2009 in Idaho presented difficulties in separating the environmental drivers from the human drivers causing change in survival rates. Previous studies on exploited populations in Alaska have estimated pooled survival around 0.55 for pack members and low survival rates ~0.38 of dispersing wolves (Person & Russell, 2008), similar to those found here in Idaho and YNP respectively, highlighting the applicability of this model to populations elsewhere. The reduced survival of dispersing wolves will be due

to the difficulties faced hunting alone, increased risk of intra-specific mortality and being forced to travel through unfavourable habitats (Marucco, 2009).

Survival rates decreased in all areas in 2008, suggesting that harsh environmental conditions occurred, and high natural mortality resulted in any anthropogenic mortality, which remained high outside of YNP, being additive (table 11, figure 6). Introduction of the hunting season may have cancelled out any delayed compensation in Idaho that should have been seen due to increased abundance of prey, newly available pack territories and possibly through increased litter size (Chapron, 2003). This trend was seen in YNP and Wyoming (figure 2).

The continued decline in survival rates in Idaho into 2010 was not expected seeing that no hunting licenses were issued. A mechanism driving this decline could be the delayed causes of pack disruption and the results of non-selective removal (Wells, 1989, Rutledge, 2010). There may also have been a rise in illegal takes due to frustrations at the removal of hunting (Treves, 2011). This will only become clear after data on consecutive hunting seasons has been collected and analysed, but with survival rates decreasing by more than 35% in 3 years, population collapses may occur before the effects of hunting are fully understood.

The decreased survival estimates for individuals targeted for collaring agrees with the previous analysis on NRM grey wolves in survival reducing in the period from 2008-2010 (figure 3). The differences in survival rates between individuals targeted for collaring and those collared for monitoring purposes decreased from the periods of 2005-2007 and 2008-2010. This could be evidence that it is increased anthropogenic mortality driving down survival in Idaho. Livestock depredation usually results in an individual being targeted for collaring. This increases the risk of illegal takes and the chance of being given consent for a licensed control action to take place as individuals who have history of livestock depredation have a higher risk of returning, usually due to overlapping territories with livestock ranches (Jaeger M.M., 2004). Low recovery probabilities for individuals collared for monitoring purposes implies that high

illegal culling may have occurred in 2008 as only 10 anthropogenic mortalities were reported (table 5) with natural mortality remaining constant but survival rate dropping.

The increased recovery probability of 0.862 (0.307, 0.569) of individuals targeted for collaring, higher than individuals collared for monitoring purposes , suggests that low survival for individuals targeted for collaring is largely due to licensed control actions and less illegal takes. Individuals that have been targeted will have been informed to the state departments as being a nuisance, locals who inform the state are probably less likely to take matters into their own hands and this may be represented in the increased recovery probability. This highlights the importance of good relationships between State managers and local communities. If the State wishes to have detailed knowledge of pack territories and to reduce the number of individuals that are lost from the population they need to build relations within the community and increase the recovery probability of individuals collared for monitoring purposes. (Zabel, 2008, St John, 2011).

Differences in survival rates between sexes of adults in Wyoming (figure 5) highlights the pressure individuals face from anthropogenic causes. During the denning season adult male survival rates decrease where as female and yearling survival rates increase (figure2). The lower increase in female survival rate in comparison to yearlings could be due to the increased mortality risk of weaning. The drop in adult male survival rate was either due to difficulties in hunting alone, provisioning for the pups (Harrington, 1983) although this is not seen in Idaho and YNP, or that female and yearling survival rates increase because they are not moving in areas of high anthropogenic mortality during that period. High survival rate in the period January through March may be delayed compensation acting given the low survival rate from October through December.

 Studies in the Alps have shown survival rates of grey wolves to increase during the winter (Marucco, 2009) furthering the argument that anthropogenic mortality is not compensatory as adults survival was found to be highest during denning

figure(2). In Idaho survival rates increased during denning for both sexes, implying that decreased natural and anthropogenic mortality occurs. Reduced natural mortality could be due to a decrease in intra-specific confrontations due to decreased movements among individuals. Recovery probability in Idaho increases significantly during the first season of denning (figure 10) suggesting that there are reduced illegal takes, although this could be due to reduced emigration out of the study area and easier tracking of individuals through decreased movement. Field studies in YNP have shown evidence of compensation in pup survival in the following year after outbreaks of distemper reduced pup survival (Smith & Almberg, 2007) but this is the first to provide evidence for compensation due to decreased survival in other age classes in the NRM. The analysis here provides evidence to support the theory that low survival is compensated for the season afterwards probably through increased prey availability.

The level of compensation due to anthropogenic mortality incurred in the three study areas highlights the importance of adjusting the amount of reported mortality to total actual mortality. Creel *et al* found most wolf data sets to be additive or super-additive (Creel, 2010) and the results here would agree with that in YNP and Idaho if the reported mortality was not adjusted. Failure to adjust total mortality while constructing management plans would result in underestimating the increase in mortality incurred through hunting, possibly resulting in unexpected and undesired population crashes.

The model predicts that off-take in Wyoming is nearly completely compensatory, however, the proportion of known natural mortality never rises above 50% in a given year and is even 0 in 2009 (table 5). These high levels of anthropogenic mortality appear to be compensated in survival rate of pups and yearlings although low adult survival rates in comparison to Idaho and YNP (figure 1) suggest that it is additive overall. Studies have shown that when anthropogenic mortality is 30% of total mortality or greater that it is additive suggesting that it should also be in Wyoming and Idaho (Sandercock, 2011).

This high level of predicted compensation does not mean that the population is at equilibrium or that density dependence is acting, only that high mortality in adults and especially old adults is compensated in high pup and yearling survival. This could be due to an increase in territory availability, decreased intra-specific competition for dispersers and/or a decrease in competition for provision provided to pups from other pack members (Harrington, 1983). Similar survival rates of adults in Idaho from 2008-2010 to those found in adult males in Wyoming, suggests compensation in pup survival in Idaho is possible. Scarcity of data did not permit separate analyses of pup survival between 2005-2007 and 2008-2010 to confirm this trend.

The density dependence reached in YNP is essential knowledge for future reintroduction programmes. The study here implies that density dependence an area the size of YNP (~3 500 sq miles) can be attained in 12 years. Higher human densities will reduce the carrying capacity of an area suggesting it could be reached even quicker in unprotected regions. Models have shown carrying capacities to be reached by wolves quickly (Miller, 2002) and this confirms that prediction.

High predicted compensation in YNP may be due to recovery probabilities being driven down by high emigration out of the study areas, violating assumption (3) of the model (section 2.2.1). This is discussed further in the section 4.3. The true level of compensation will lie somewhere between that of the unadjusted and adjusted predictions (figure 11). This is another indicator of density dependence acting and if we assume that the proportion of unknown mortality which is of anthropogenic causes are similar to that of the known deaths (0-25%) (table 5), then anthropogenic mortality is partially compensatory, similar results were found previously in the NRM (Murray, 2010).

Similar issues arise with recovery probabilities and compensation in Idaho, with the lack of natural mortality. Compensation will lie somewhere between that of the adjusted and unadjusted predictions given that dispersal into Montana from Idaho is known to be high. The proportion of known mortality that is natural never exceeds 20% and only makes up 7 % of known mortality throughout the

study. At low levels compensation will be predicted as anthropogenic mortality is always occurring before natural mortality. If the majority of unknown deaths are of anthropogenic causes, which may be reasonable assumed, given that unreported deaths will have a higher probability of being illegal takes, then the effect is predicted to be additive.

4.2 Management Implications

Low survival rates of adult males in Wyoming make the population susceptible to increased anthropogenic mortality through loss of breeding pairs, even though grey wolves are seen as very resilient animals (Weaver, 1996). The additive nature of human caused mortality in Idaho shows how an increase in off-take could drive survival rates lower than they already are. This is of particular concern in Wyoming were the number of breeding pairs could dramatically decrease as compensation is only seen in pup and yearlings and not in reproducing adults. Studies on the red wolf have shown loss of breeders to decrease litter size which could mean that high pub survival is misleading in terms of total number recruited to reproducing adults (Sparkman, 2011). The possibility of reduced litter size with the low survival rate of adults and lack of old adults in Wyoming which is not experiencing density dependence may be a cause for concern although pooled survival rate of 0.62 is at the lower bound of a stable population (Fuller et al., 2003). The apparent stable population in YNP will continue to provide a source for Wyoming's population offsetting the low survival rates and it has been shown in models under low migration that disjoint populations can be sustained (Haight, 1998).

The impact of a harsh year on survival combined with a hunting season the following year appear to have increased overall mortality in 2010 (figure 7) even though relisting occurred. This may be of concern when hunting occurs annually, oppressing compensation following years of low survival, putting population viability may be put at risk.

The population in YNP appears to have exceeded carrying capacity in 2007 and the compensation in 2009 after a large drop in survival suggests that survival

rates will level off between 0.6-0.65 overall. Variance in this will occur as harsh years and low survival rates are followed by compensation the following year either through increased prey abundance or decreased intra-specific mortality. Low emigration exhibited between YNP and Idaho (1 individual) suggests another protected source is required with greater dispersion if the population in Idaho is to persist under increased anthropogenic mortality.

Smith *et al.* highlighted the importance of Idaho as a source for the population in Montana (Smith et al., 2010). High off-take rates encourage immigration from elsewhere (Robinson, 2008) where survival is higher. Reduced survival rate in Idaho would reduce migration between the two putting both populations at risk (Novaro, 2005, Cooley, 2009). The NRM is a great example of how migrations can sustain heavily exploited populations but this requires the sources to maintain migration (Haight, 1998). Caution must be taken in the initial years of hunting as this analysis shows (figure 1) that increased mortality two years running can oppress compensation the following year and result in further decreases in survival rate. Given that Idaho is a known source for Montana makes this increases the consequences of decreased survival rates.

Mortality rates of >0.38 have been shown to result in decreasing populations (Chapron, 2003, Fuller et al., 2003). Wyoming does provide evidence that this decrease in adult survival can be compensated in pup survival but it does leave the population susceptible to a loss of breeding pairs (Sparkman, 2011) and reduced kinship in packs, which has been shown to decrease fitness (Rutledge, 2010). Higher emigration from YNP to Wyoming (16 individuals) possibly compensates for reduced survival and both YNP and Wyoming appear sustainable at current survival rates (Cooley, 2009).

To increase the understanding of compensation relationship between pups and adults it would be beneficial to target pups for collaring and increase the data available to enable detailed and time-variant analyses of pup survival.

4.3 Analytical Issues Potentially Influencing Results

Table 6. Annual sampled population size, number of individuals going missing and number recovered dead annually in the three study areas.

	YNP			Idaho			Wyoming			Collar loss
	$\hat{N}_Y$	$\sum_{i=1}^{N_y} v_{i,Y}$	$\sum_{i=1}^{N_Y} d_{i,Y}$	$\hat{N}_Y$	$\sum_{i=1}^{N_y} v_{i,Y}$	$\sum_{i=1}^{N_Y} d_{i,Y}$	$\hat{N}_Y$	$\sum_{i=1}^{N_y} v_{i,Y}$	$\sum_{i=1}^{N_Y} d_{i,Y}$	
Released Jan-2005	70			66			24			
Y=**2005**	71	4	15	93	8	12	31	4	8	1
2006	67	9	6	110	8	16	38	8	11	5
2007	61	10	8	114	14	16	50	9	9	7
2008	61	10	19	113	17	37	48	13	22	7
2009	49	6	9	122	27	36	53	5	7	3
2010	47	9	5	80	26	27	60	12	18	7
Alive in 2010 Sept-Dec	28			44			34			

Mark-recapture-recovery models are usually performed over the entirety of the data set to hand. The brevity of the study here may result in overestimation of survival due to the fact that individuals are required to be released into the study (see section 2.2.1). In the first season of 2005 any individuals that died were removed from the study as never being released. That left only two options for this period, either an individual was never seen again and its fate during that season was unknown, or it was deemed to have survived as it was recaptured at a later date. This resulted in 5% of the seasons analysed being mortality free, however, survival rates estimated here did not appear to differ from those of the following seasons. Other individuals whom were collared prior to 2005 and only recovered dead during the study period but never recaptured were omitted for the same reason. This removed individuals whose recapture probabilities were low and may have resulted in increasing them. This again will impact on survival rates as individuals that go missing from the population must be accounted for using the χ term in equation (1, section 2.2.1).

73 individuals were removed due to never being released into the study, mostly removed from Idaho (table 7). The impact these will have had on recapture rates in YNP and Wyoming was insignificant as only 9 individuals were removed all together due to either mortalities in season 1, never being captured during the study or mortalities before initial capture. 64 individuals were removed from Idaho of which 3 were removed due to mortalities in season 1 and 29 were never captured or only recovered dead. The decrease in recapture rates from 0.912 in 2005 to 0.861 in 2007 and down to 0.792 suggests that recapture rates were inflated at the beginning of the study due to the removal of individuals. Taking 0.792 to be the true recapture rate in Idaho did not significantly vary survival rate estimates (<0.1%). It can be safely assumed therefore that survival rates were not impacted due to this bias in recapture probabilities.

Table 7. Individuals removed from the analysis due to missing covariates, never being released into the study either due to being missing throughout or recovered dead before being recaptured having been marked during the previous study.

	YNP	Idaho	Wyoming
Never Released	0	31	0
Only Recovered Dead	3	35	5
Missing Covariates	0	12	1
Included in Study	167	296	166
Total In Study	613 (16 migrations between study areas)		

Changing the time step to one year increased survival rate estimate to 0.719 from 0.682 in YNP with similar increases in Idaho and Wyoming. This was due to the fact that 38 individuals had to be removed from the analysis as they died in 2005, others that died in the same year as their release will also have been removed, biasing the data towards individuals that survive at least one year. The assumptions of the model would need to be changed if individuals that die in the year of their release were to be incorporated but this shows the effect removal of dead recoveries may have had on survival in the first three months and other seasons where omitting individuals occurred. Removing only

individuals that were never captured during the study gave overall survival estimates of 0.680, 0.607 and 0.628 in YNP, Idaho and Wyoming, respectively. The effect on YNP and Wyoming was insignificant as only 8 individuals were removed altogether. The survival estimates in Idaho decreased by 4% suggesting that inflation may have occurred due to removal of these individuals. This problem is exaggerated here because of the brevity of the analysis. In long term analyses this initial error would be less dominant and reporting rates of collar failures may increase as individuals have a higher probability of being recaptured and known to be without a working collar. The overestimation in Idaho is likely to have occurred at the beginning of the study suggesting that the high survival rates in Idaho from 2005-2007 may be misleading. Later on in the study individuals had a higher probability of being previously recaptured so these survival rates may be closer to the true values.

Overestimation in recapture probabilities may also have been offset by emigration out of the study area and tag loss (information was only provided in Wyoming on tag loss). It was assumed that the populations were closed which is a reasonable assumption between the three states of Idaho, Wyoming and Montana. The exclusion of Montana due to a delayed completion of the data-set may have resulted in emigration being greater than could be safely ignored. This will have impacted on both recovery and recapture probabilities driving them down. Details of tag loss were not provided in Idaho or YNP but using Wyoming as a reference where 6% of collars where known to fail we could explain some of the apparent loses from the population. ~30% of individuals were lost during the study in Idaho and YNP leaving 25% still to be explained. Given that Montana is a known sink (Smith et al., 2010) it is reasonable to assume that these were not all unreported mortalities but migrations into Montana. Dead recoveries were reported outside of the study areas in Canada and Montana in the Idaho data set and prior to 2005 had been reported in Utah and Colorado. This suggests that recovery probabilities may not have suffered as a consequence of violating this assumption and it is shown above that even bias in recapture probabilities does not significantly bias survival rate estimates.

The variation and low level of recovery probabilities in YNP could be attributed to emigration out of the study area. This would explain the significant seasonal variation as certain seasons will have higher emigration rates. It also points towards density dependence as this can result in high emigration rates due to lack of food and social cramping (Sinclair, 1996).

Models exist to incorporate temporary emigration out of study areas where recoveries can be made both inside and outside of areas where recapturing takes place (Barker, 2004, Lindberg, 2001), however this requires knowledge of whether an individual was seen alive in the study area prior to recovery and this was not provided.

The construction of the model may also have affected survival rates in 2010 due to the fact that individuals that were not recovered dead in the final season could not be confirmed to have survived it. Therefore the only contributions to the log likelihood function defined in (1) came from mortalities. This could have decreased survival rates in 2010 as the number of individuals that in fact survived until 2011 were not all included as survivors. Survival rate during the period October through December was consistently lower in all three areas throughout the study and survival rates from January through September in 2010 were lower than in 2009 suggesting that the annual survival rate estimate in 2010 was accurate.

Acknowledgements

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Appendix

A.1

1984-2004 Comparison

USFWS requested a comparison be made of the methods used above and those used by Smith *et al.* previously. Data provided from 1984-2004 detailed Mark-Recovery and loss from the study population. This did not permit analysis of recapture rates which presented problems using the likelihood estimator defined in section 2.2.1 and comparing this analysis with the Cox Proportional Hazards used before (Smith et al., 2010, Andersen, 1982).

Figure 7 shows the annual survival estimates produced with recapture rates set at 1. It is reasonable to assume that recapture rates will have been high ~1 in Idaho immediately after the reintroduction and decreased as the population expanded.

Pooled survival was estimated at 0.685 (0.660, 0.707) using MRR methods with recapture probability fixed at 1 and 0.688 (0.664, 0.711) using recapture probabilities found from 2005-2010 in Idaho and a hypothesised value for N.W. Montana of 0.7. This compared with the previous analysis estimate of 0.75 (0.728, 0.772). Individuals that went missing from the study areas were right censored back to the last known time that they were alive in the population in the previous analysis. No information was given on the failure of collars so no individuals were censored using the MRR methods. This right censoring of individuals that went missing could overestimate survival by removing individuals that had died in the study area, but not been reported, from the analysis. This would be caused by removing mortalities from the population but including the time the individuals survived even though homogeneity of recapture and recovery probabilities among individuals assumption had not been violated (see section 2.2.1). It would be of interest to note the difference in survival estimates that would have occurred by removing these individuals from the analysis completely. If all individuals that went missing from the study were

right censored then the likelihood estimator (1) collapses into a binomial model which predicts pooled survival to be 0.8. This suggests that if collar failures were incorporated into the model then the survival estimate would lie between 0.69 and 0.8 which would be in the region of the previous analysis.

The previous analysis also assumed that survival rates did not decrease throughout the study. Figure 7 shows that survival rates dropped in Idaho during the study such that the pooled survival estimate would not have been a valid estimate of survival rates after the year 2000. This provides insight into the short term effects on survival rates during re-colonisation. Caution should be taken when comparing the results provided in figure 7 with those provided in this analysis. The Greater Yellowstone Recovery Area is not completely protected land as is in YNP so survival rates may have been lower outside of the park than inside. The effect of recapture rates on survival is greater in smaller populations which implies that survival estimates here may not be accurate. They do provided evidence of trends though and it is easy to see that survival in GYA was varying around 0.7, similar to that found in my study from 2005-2007.
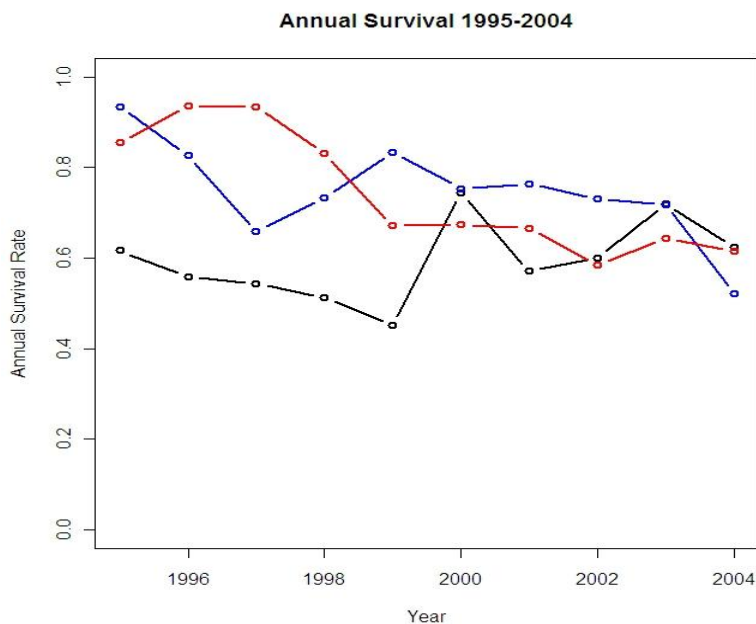

Figure 7. Annual survival rates from 1995-2004 calculated using MRR methods defined in section 2.2.1, recapture probability =1
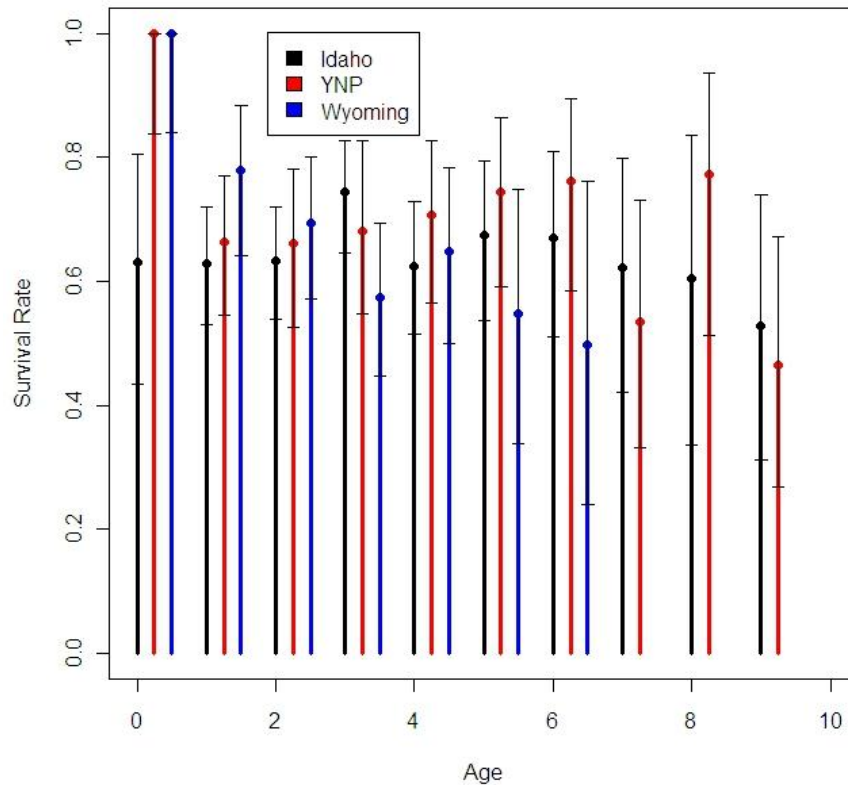
A.2

Age Specific Survival

Figure 8. Age specific annual survival rates in the 3 study areas, pup survival given is 3 months and survival rates are only given for 1-5 and 6+ yr olds in Wyoming.

Exact age was known or estimated through genetic sampling in the Greater Yellowstone Area and roughly estimated in Wyoming and Idaho if unknown. The lack of precise ages in Idaho did not enable this to be incorporated into the analysis above so is provided here as an estimate of age specific survival. Age estimates were taken to be the mid value of the estimate provided and rounded down for were the mid value was not an integer.