ATTACHMENT A

To the Written Evidence of

Raincoast Conservation Foundation

Population Viability Analyses

for

Southern Resident Killer Whales

Prepared for Raincoast Conservation Foundation

By Dr. Bob Lacy, Dr. Paul Paquet and Misty MacDuffee

December 5, 2018

Summary of key conclusions from the 2015 report submitted previously as evidence to NEB

In 2015, we submitted a report in which we presented the results of a population viability analysis (PVA) of the risk associated with aspects of the proposed Trans Mountain Expansion Project (Project) on the endangered Southern Resident Killer Whales ("Southern Residents") (Lacy et al., 2015). A PVA is a risk management tool, which models the risk to a population over time. In this case, the model was used to estimate the increased risk to the Southern Residents from three threats associated with the marine shipping component of the Project: an oil spill, increased acoustic and physical disturbance from ships, and ship strikes. The report also examined the possible effects of decreased Chinook salmon prey base that might result from climate change or human activities, and evaluated those impacts in comparison to the more immediate threats of the proposed Project and as the environmental context within which the impacts of the Project are likely to occur. We present here a brief synopsis of the findings of the 2015 report and present the findings of subsequent work conducted in 2017 (Lacy et al. 2017) and again in 2018.

Summary of 2015 PVA report

Based on status quo conditions, the Southern Resident population was projected to remain about at its current size or continue a very slow decline (estimated at a mean annual decline of 0.2%). We projected a 9% chance of quasi-extinction, where the population falls below 30 whales and is no longer viable. Sensitivity tests, in which alternative values for model inputs were examined, showed that the prediction of no population growth or slow decline was robust within plausible ranges of demographic rates. Thus, under status quo conditions the population cannot be expected to recover from its current endangered status.

Any additional negative pressures would cause decline, further threaten the persistence of the population, and make recovery more difficult to achieve through positive action. Reducing the abundance of Chinook salmon was projected to have a substantial negative impact on the Southern Residents population. Conversely, increasing Chinook abundance can lead to relatively robust population growth (up to 1.9% with 20% more prey) and protection from extinction or serious decline.

Our analyses showed that the Project will intensify existing threats, accelerating the rate of decline in the Southern Residents and possibly leading to a complete extinction. The impact of oil spills on long-term population growth could be consequential. The probability of the population dropping to quasi-extinction (i.e. below 30 whales) due to an oil spill is substantial, with a possibility of complete extinction within 100 years due to the potential of catastrophic decimation of the population to a small and unrecoverable number from which it could not recover. The modeled impact of noise and physical disturbance accompanying increased or added vessel traffic associated with the Project resulted in accelerated population decline, smaller mean population size, and increased probability of complete and quasi extinction. The cumulative impact of oil spills, increased noise, and incidental human caused deaths resulted in a population decline of more than 1% per year, resulting, in the next 100 years, in: a mean final population size of only 33 animals; a 8.6% probability of complete extinction of the Southern Residents; and more than 50% probability that the final population would be less than 30 animals and, therefore, probably on a course toward nearly inevitable extinction.

Citation: Lacy, R.C., K.C. Balcomb III, L.J.N. Brent, D.P. Croft, C.W. Clark, and P.C. Paquet. 2015. Report on Population Viability Analysis model investigations of threats to the Southern Resident Killer Whale

population from Trans Mountain Expansion Project. Attachment E, Ecojustice – Written Evidence of Raincoast Conservation Foundation (A70286), National Energy Board (Canada). 120 pp. Available at http://docs.neb-one.gc.ca/fetch.asp?language=E&ID=A4L9G2.

Note that two references that document impacts of disturbance on killer whales were omitted from the prior submission to NEB. For completeness, these references are provided here:

Bain, D. 2002. A model linking energetic effects of whale watching to killer whale (*Orcinus orca*) population dynamics. University of Washington, Friday Harbour, WA 98250.

Williams, R., D. Lusseau, and P. S. Hammond. 2006. Estimating relative energetic costs of human disturbance to killer whales (*Orcinus orca*). Biological Conservation 133:301-311.

Summary of conclusions from PVA projections conducted subsequent to the 2015 report and published in 2017

Subsequent to the report submitted to the NEB in 2015, we added several more experts to our team and extended the above analyses. We considered additional scenarios that included a model of no anthropogenic threats (no noise disturbance, no PCB contaminants, no oil spill or ship strikes from shipping activities, and no change from the long-term mean prey abundance), and two scenarios that considered effects of the Project in conjunction with projected declines in prey abundance. We also projected the benefits that would arise from improvements in Chinook abundance, noise disturbance, and PCB contaminants, and estimated what level of improvements to these threats would be required to achieve a USA recovery target of sustained 2.3% growth over 28 years.

These analyses of threats and potential mitigation actions were published in the highly respected, peer-reviewed journal Scientific Reports, October 2017 (Lacy et al. 2017) (Appendix A). A brief synopsis of those findings is presented here as context for the further analyses to be described below.

The published analyses confirmed that the Southern Resident population is fragile, with no growth projected under current conditions, and decline expected if new or increased threats are imposed. “Lower increase” and “Higher increase” scenarios that modelled increased threats expected with the Project in conjunction with expected declines in Chinook abundance projected Southern Resident population declines (1% and 2%) that bracketed the projections from the Cumulative effects scenario of the PVA submitted previously to NEB. Similarly, the probability of the population falling below 30 animals (quasi-extinction) in the new development scenarios (31% and 70%) bracketed the 54% quasi-extinction probability that had been estimated for Project impacts.

A scenario that removed all anthropogenic threats confirmed that in the absence of such threats, and with prey at the mean levels observed in recent decades, the population would respond with about 2% mean annual growth and have little chance of serious decline or extinction. Analyses that examined the recovery expected with plausible reductions in threats and improvements in the habitat showed that prey limitation was the most important factor affecting population growth in the models. However, to meet recovery targets through prey management alone, Chinook abundance would have to be sustained near the highest levels since the 1970s. The most optimistic mitigation of noise and contaminants would make the difference between a declining and increasing population, but would be insufficient to reach recovery targets. As one example of a multi-pronged approach that could achieve recovery, reducing acoustic disturbance by 50% combined with increasing Chinook by 15% was projected to allow the population to reach 2.3% growth. The actions that would be required to achieve recovery will need to be greater if the Project or other development activities add to the existing threats that have prevented recovery to date.

Citation: Lacy, R.C., R. Williams, E. Ashe, K.C. Balcomb III, L.J.N. Brent, C.W. Clark, D.P. Croft, D.A. Giles, M. MacDuffee, and P.C. Paquet. 2017. Evaluating anthropogenic threats to endangered killer whales to inform effective recovery plans. Scientific Reports 7:14119. doi: 10.1038/s41598-017-14471-0.

Updated Population Viability Analyses 2018

The evidence submitted previously to NEB in 2015 and the published 2017 PVA described above were based on demographic data accumulated from 1976 through 2014. Subsequently, the SRKW population has continued to be monitored, and demographic data are now available up through October 2018 (Table 1). It is worthwhile to re-examine the population trajectories predicted by the PVA because:

- The additional almost 4 more years of data can improve our estimates of average demographic rates and variability in rates.
- The recent decline (from 78 to 74 killer whales from the beginning of 2015 through to today) should be investigated to determine if the poor demographic trend of the past few years is within the range of annual fluctuations projected by the prior models, or instead indicates that the population has entered into a new phase of demographic decline.
- Regardless of whether the recent patterns signal a new trend or just some unlucky years within the long-term pattern, with the expanded data set based on more years of monitoring, the conclusions about current viability, impacts of threats, and prospects for recovery with new management actions should be revisited to see if prior conclusions are still deemed valid.

Table 1. Population age and sex structure from 1980 to October 2018 in five year intervals for Southern Resident Killer Whales. Data source: Fisheries and Oceans Canada – Cetacean Research Program (unpublished)

YEAR	Total	Reproductive Females (>10 years)	Adult Males (>10 years)	Post Reproductive Females (>42 years)	Juveniles (<10 years)
2018	Total: 74 J Pod 22 K Pod 18 L Pod 34	Total: 27 (36%) J Pod 10 K Pod 6 L Pod 11	Total: 23 (31%) J Pod 4 K Pod 8 L Pod 11	Total: 5 (7%) J Pod 1 K Pod 1 L Pod 3	Total: 6F, 13F (26%) J Pod 2F, 5M K Pod 1F, 2M L Pod 3F, 6M
2017	Total: 76 J Pod 23 K Pod 18 L Pod 35	Total: 27 (36%) J Pod 10 K Pod 6 L Pod 11	Total: 24 (32%) J Pod 4 K Pod 8 L Pod 12	Total: 5 (6%) J Pod 1 K Pod 1 L Pod 3	Total: 7F, 13M (26%) J Pod 3F, 5M K Pod 1F, 2M L Pod 3F, 6M
2015	Total: 80 J Pod 27 K Pod 19 L Pod 34	Total: 30 (37%) J Pod 12 K Pod 6 L Pod 12	Total: 23 (29%) J Pod 5 K Pod 8 L Pod 10	Total: 5 (6%) J Pod 1 K Pod 2 L Pod 2	Total: 8F, 14M (27%) J Pod 4F, 5M K Pod 1F, 2M L Pod 3F, 7M
2010	Total: 84 J Pod 26 K Pod 19 L Pod 39	Total: 30 (36%) J Pod 10 K Pod 7 L Pod 13	Total: 17 (20%) J Pod 4 K Pod 3 L Pod 10	Total: 9 (11%) J Pod 2 K Pod 1 L Pod 6	Total: 9F, 19M (33%) J Pod 5F, 5M K Pod 2F, 6M L Pod 2F, 8M
2005	Total: 88 J Pod 24 K Pod 20 L Pod 44	Total: 32 (36%) J Pod 8 (K Pod 9 L Pod 15	Total: 20 (24%) J Pod 4 K Pod 3 L Pod 13	Total: 11 (12%) J Pod 2 K Pod 2 L Pod 7	Total: 9F, 13M (27%) J Pod 6F, 4M K Pod 1F, 5M L Pod 2F, 6M
2000	Total: 77 J Pod 19 K Pod 16 L Pod 42	Total: 28 (36%) J Pod 6 K Pod 7 L Pod 15	Total: 11 (14%) J Pod 1 K Pod 1 L Pod 9	Total: 12 (16%) J Pod 2 K Pod 2 L Pod 8	Total: 11F, 15M (34% J Pod 5F, 5M K Pod 2F, 3M L Pod 4F, 7M
1995	Total: 92 J Pod 20 K Pod 18 L Pod 54	Total: 34 (37%) J Pod 10 K Pod 8 L Pod 16	Total: 14 (15%) J Pod 3 K Pod 1 L Pod 10	Total: 12 (13%) J Pod 2 K Pod 3 L Pod 7	Total: 15F18M (36%) J Pod 2F, 3M K Pod 4F, 3M L Pod 9F, 12M
1990	Total: 87 J Pod 18 K Pod 16 L Pod 53	Total: 33 (38%) J Pod 9 K Pod 8 L Pod 16	Total: 17 (19%) J Pod 4 K Pod 3 L Pod 10	Total: 11 (13%) J Pod 2 K Pod 1 L Pod 8	Total: 12F, 7M (30%) J Pod 2F, 1M K Pod 3F, 1M L Pod 7F, 5M, 7?
1985	Total: 74 J Pod 17 K Pod 14 L Pod 43	Total: 31 (42%) J Pod 7 K Pod 7 L Pod 17	Total: 16 (22%) J Pod 3 K Pod 3 L Pod 10	Total: 9 (12%) J Pod 2 K Pod 2 L Pod 5	Total:8F, 8F (24%) J Pod 4F, 1M K Pod 2F, 0M L Pod 4F, 7M

1980	Total: 79 J Pod 18 K Pod 16 L Pod 45	Total: 25 (32%) J Pod 5 K Pod 5 L Pod 15	Total: 13 (16%) J Pod 3 K Pod 4 L Pod 6	Total: 11 (14%) J Pod 3 K Pod 3 L Pod 5	Total: 18F, 12M (38% J Pod 5F, 2M K Pod 3F, 1M L Pod 10, 9M

The updated analyses incorporating the data from the past four years confirmed that the population is fragile and perhaps in a slow decline, with no ability to withstand additional threats and an inability to recover unless current conditions are improved. The decline of the past four years is not outside of the bounds of uncertainty from the projections that were made previously, but the recent lack of successful reproduction could be an indication that conditions have deteriorated. With the revised estimates of demographic rates, we now estimate that the Project would cause 1.6% to 2.3% annual decline, about 0.5% per year faster than estimated using the older data. The likelihood of the population falling below a functional extinction threshold of 30 killer whales is now estimated to be greater than was projected before.

Methods

Following the same statistical methods that were used previously with the 1976-2014 dataset, but now with additional data from 2015 through late 2018, fecundity (probability of producing a calf in a given year) was calculated for young mature females (ages 10-30y; 0.1183) and older mature females (ages 31-45y; 0.0747). Annual mortality rates were calculated for calves (up through 1 y of age; 20.81%), subadults (1 to 9 y; 2.44%), young mature females (ages 10 to 30y; 0.97%), older mature females (ages 31 to 45y; 2.35%), post-reproductive females (46 to 90y; 7.75%), young mature males (10 to 21y; 3.03%), and older males (22 to 90y; 8.85%). We applied these updated estimates of demographic rates to the Baseline and Cumulative effects models in the Lacy et al. (2015) evaluation of Project impacts, and to the primary models of the SRKW population that were examined in the Lacy et al. (2017) publication. Given that the adjustments to demographic rates were small, we have not repeated all the sensitivity tests on each model input parameter, as was done in the earlier PVA.

Recent evidence suggests that inbreeding might be becoming common in the small SRKW population, but the demographic consequences of that inbreeding are not yet clear (Ford et al. 2018). In our models, we assumed that parent-offspring mating would be avoided, but that paternal half-siblings could mate. Sensitivity tests indicated that the effect of varying severity of inbreeding depression had relatively small impact on population projections, perhaps because we assumed that very close inbreeding was avoided. If inbreeding becomes more frequent than assumed in the PVA, then population declines could be exacerbated increasingly as the number of breeders continues to decline.

The revised population model was started with the population structure (age and sex distribution and, when known, the parentage of individuals) of the current (November 2018) population of 74 SRKWs. In tests of impacts of existing or potential threats, and of possible management actions to achieve recovery, we initially applied the same functional relationships as used before to describe the demographic effects of prey abundance, noise disturbance, PCB contamination, oil spills, and ship strikes. See Lacy et al. (2015; 2017) for details of the PVA model structure and parameter values.

The strength of the relationships between prey abundance and demographic rates (both fecundity and survival) are uncertain, because the Chinook salmon stocks that are most critical for the SRKWs are uncertain, estimates of prey abundance are imprecise, and the observed correlations between salmon indices and SRKW demography might reflect dependency of both on some other factors rather than only a causal relationship between prey and demography. We therefore examined also population projections that assumed 50% increase in the slopes[1] of the prey-demography relationships, and projections that assumed 50% lower slopes. In these scenarios, intercepts of the mathematical relationship were adjusted so that the demographic rates remained unchanged when the index of prey abundance was 1 (i.e., the long-term mean prey abundance).

Results

Our updated "Baseline" population model, representing our estimate of the population dynamics under current conditions, projects a mean population growth of r = -0.006, or 0.6% decline per year, with variation across years of SD(r) = 0.047. This compares to projections of mean r = -0.002 (0.2% decline per year), SD(r) = 0.042 in the earlier analysis (Lacy et al. 2015 2017). The lower revised estimate results from the poor reproduction and calf survival over the last three years. Note that if the reduced fecundity and calf survival of the past few years represents a new norm for the population, rather than three poor years that should be averaged into a longer term trend of mostly better reproductive success, then the projections for the future population growth will be considerably worse than what we present here.

The observed population decline of 4 whales since 2014 has averaged 1.3% per year (r = -0.013, SD = 0.062). Thus, the population has declined at a faster rate than the mean projected in the PVAs, but the observed rate is well within the range of annual fluctuations that was predicted. For example, the population model based on data through 2014 (Lacy et al. 2017) projected a 30% probability that the population would decline by 4 or more whales by the end of 2018.

Although the overall recent population decline is within the range that can occur with the estimated demographic rates, the lack of successful reproduction in the past 3 years (2016-2018) is atypical and cause for concern. Two births occurred in that time but neither calf survived. Since 1976, only once before has there been a sequence of three years (1981-1983) in which only 2 births occurred. There has been no equivalent period, however, where complete reproductive failure was documented (i.e. no new and surviving progeny). The mean number of offspring expected over the past 3 years, given the number of mature females in the population, is 9.

We compared projected population growth from the earlier studies to the same models with the updated estimates of demographic rates (Table 2). Across the scenarios that were examined, the revised demographic rates led to about 0.5% slower population growth (or 0.5% faster decline in the cases of negative growth). This is a relatively small effect on a year-to-year basis, and the effect would not be detectable statistically in just a few years of data. However, when projected over 100 years it results in notable increases in the probability of complete extinction of the population and in the probability of

---

[1] In mathematics, the slope or gradient of a line is a number that describes both the direction (plus or minus) and the steepness of the line that describes the relationship between two variables. Thus, slope is the 'steepness' of a line which shows the rate of positive or negative change of a variable as a consequence of the change in a causal variable. If the slope is 50% greater, then a given increment in the causal factor (e.g., prey abundance) will cause 50% more change in the consequences. A 50% lesser slope means that the same change in the causal factor will cause half as much change in the responding variable.

declining below a population size of 30 (approximately the size of a single pod, a plausible definition of function extinction of the population).

Table 2: Measures of viability of the SRKW population over 100 years under scenarios of minimal anthropogenic threats, current threats, two levels of increased threats due to development, and a model of the cumulative direct impacts of the Project. Projections using data through 2018 (upper values in each pair of results, in bold) are compared to projections using data through 2014 (lower values in each pair). Top four scenarios compare current projections to those reported in Lacy et al. 2017. Last scenario compares current projection for the Cumulative effects scenario reported for the Project in Lacy et al. 2015.

	Threats modelled					**Population projections**		
Scenario	Chinook trend	Noise	PCB (ppm/y)	Oil spill (big; small)	Ship strikes[2]	Population growth (r)	Probability extinct	Probability final N < 30
No anthropogenic threats	constant	0	0	0	0	**0.015** 0.019	0 0	0 0
Current threats	constant	85%	2	0	0	**-0.006** -0.001	1% 0	25% 5%
Low increase	-25% in 100y	92.5%	2	0.21%; 1.08%	1 per 10y	**-0.014** -0.008	13% 5%	67% 31%
Higher increase	-50% in 100y	100%	2	0.42%; 2.16%	2 per 10y	**-0.023** -0.017	43% 25%	90% 70%
Cumulative Project impacts	constant	100%	2	0.21%; 1.08%	1 per 10y	**-0.016** -0.012	17% 9%	76% 54%

Figure 1 below compares the mean trajectory of the updated baseline scenario (solid line) to the trajectory predicted in the prior analyses (dashed line), presented as mean projected population sizes (black lines) and standard deviations (grey lines) around those projections representing the uncertainty

[2]Since the 2015 submission, Southern Resident killer whale J34 (Double Stuff) died of blunt force trauma in 2016. Although collisions between whales and vessels are relatively rare, when they do occur they can cause significant injury or death (Ford et al. 2000). A science based review of the effectiveness of recovery measures for Southern Resident Killer Whales conducted in 2017 identified vessel strikes as an emerging threat to Southern Resident population that was not recognized previously (DFO 2017, Fisheries and Oceans 2018).

in the future sizes. The starting population size in 2018 for the updated projections is approximately 1 standard deviation (SD) below the mean projection made from the conditions in 2014. Thus, we do not have reason to reject the earlier baseline model as inconsistent with subsequent data, although our best estimate based on the extended data set is more pessimistic.

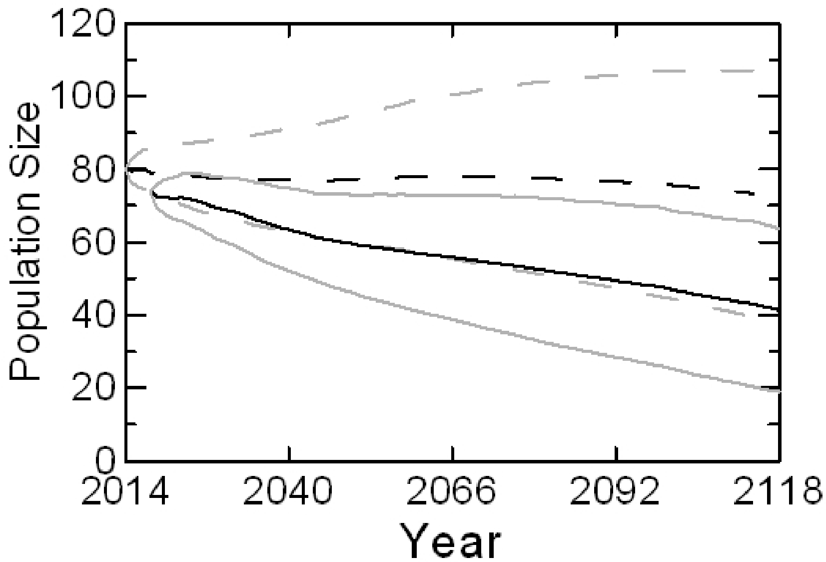

Figure 1. The distribution of simulated trajectories with mean (black) and ± 1 SD (grey) of the population size for SRKWs projected for 100 years. Dashed lines are from model using data through 2014 (from Lacy et al. 2017). Solid lines are from the updated model using data through 2018.

Figure 2 below compares the previous to the revised projections for population growth with reductions in the threats that have been identified as priority concerns in the recovery plans. With the lower projected current population growth, more reduction in threats (or alternative offsetting recovery actions) will be needed to achieve recovery goals. For example, with the updated demographic data, we no longer predict that even a 30% increase in prey abundance would achieve the 2.3% sustained growth that is a goal of the US recovery plan for the SRKW population.

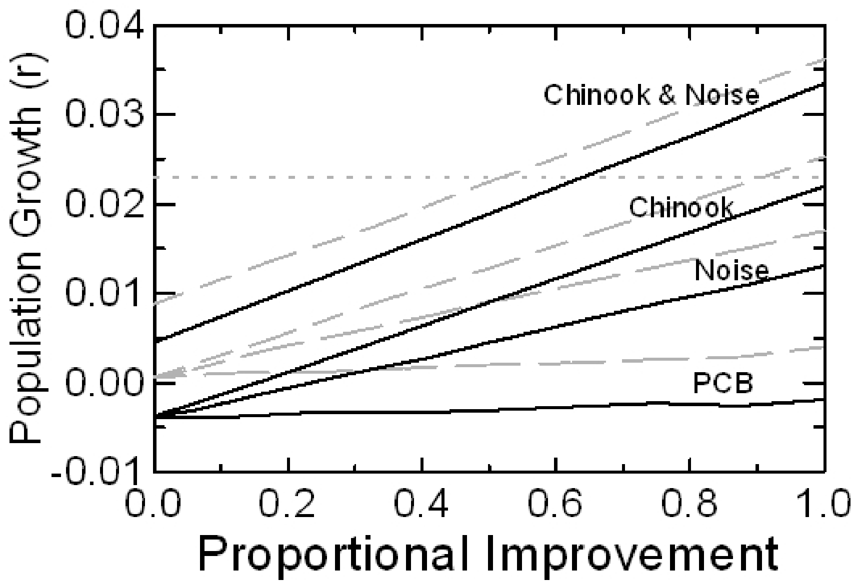

Figure 2. Mean population growth for SRKW achieved by mitigation of anthropogenic threats. Threat reductions are scaled on the x-axis from no reduction to the maximum reductions tested: Chinook abundance increased up to 1.3x the long-term mean; noise disturbance during feeding was reduced from 85% to 0; and PCBs were reduced from accumulation rates of 2 ppm / y to 0. The top lines shows growth rates under a combination of varying levels of improved Chinook abundance plus mitigation of noise to half the current level. Grey dashed lines are from model using data through 2014 (from Lacy et al. 2017). Solid lines are from updated model using data through 2018. Grey dotted line indicates a 2.3% growth rate that is a recovery goal in the US Recovery Plan.

As was shown in the prior analyses, recovering the SRKW population to the target level of population growth with reductions in any one threat will be difficult. Figure 2 illustrates one combination of actions that might achieve the desired recovery: With the updated model, we now predict that if noise disturbance is reduced by half, an increase in prey abundance of about 20% (as opposed to the 15% that was estimated in the prior model) would result in recovery with the targeted growth rate. Other combinations of recovery actions might be as or even more effective. Clearly, however, if the baseline conditions are currently worse than estimated from the past 4 decades of monitoring, or if they become worse due to ongoing and increasing anthropogenic activities (as in Table 1), then the extent of improvements necessary to recover the population will be greater than illustrated by the examples in Figure 2.

The results from models that examined population projections under assumptions of higher or lower slopes to the functional relationships between prey abundance and demographic rates are shown in Table 2 below. If anthropogenic threats could be removed, then a stronger relationship between prey and demography leads to greater population growth, and a weaker relationship leads to lower growth. This occurs in the model not because of the abundance of prey (which is kept at an index of 1.0 in these “No threats” scenarios), but rather because under an assumption of no noise disturbance the prey are more accessible to the killer whales. (The impact of noise is modeled via only its effect on feeding rates, as other possible impacts of noise have not been quantified.) Under the Current Threats scenarios, the slopes of the relationships of prey to demography have no impact on our projections (with the small differences in results being due to random fluctuations in population growth), because neither the prey abundance nor the noise levels are changed from the average values under which the demographic rates were estimated. If threats are increased (including modeling fewer prey and more noise), then an increase in the slopes of the prey—demography relationships leads to lower growth (i.e., faster decline), and greater probability of the population declining below 30 animals or even to extinction. The change in results is very small for the scenarios with low increases in threats, and not very large when higher increases in threats are modeled. Thus, across the range of plausible relationships between prey and demographic rates, the conclusion is robust that additional damage from the Project or other developments would significantly harm the prospects for SRKW persistence and recovery.

If the relationship between prey abundance and SRKW demography is stronger or weaker than has been estimated, then any declines in prey could cause the population to decline faster or slower, respectively, compared with the PVA projections. Conversely, a stronger relationship would allow for more rapid population recovery if the prey abundance can be raised to levels above the mean of recent years. When we tested 50% lower or 50% higher slopes for describing the relationships between prey abundance and demography, the effects on population projections under scenarios of increased threats were changed by relatively small amounts (Table 2). This indicates that these projections of decline under scenarios of increased threats resulting from the Project are not highly sensitive to strength of the prey-demography relationships included in the model. However, in models of improved prey abundance, the strength of the relationships had a potentially large effect on the population growth rate that could be achieved if prey abundance were increased (Figure 3). In other words, abundance and availability of prey has a much stronger influence on growth of the population than on decline of the population. Similarly, greater improvements in population growth would be observed if the prey-demography links were stronger than has been estimated and if noise was reduced, because the effect would be to increase access to prey by the killer whales.

Table 2: Measures of viability of the SRKW population over 100 years under scenarios of minimal anthropogenic threats, current threats, two levels of increased threats due to development, and a model of the cumulative direct impacts of the Project, under different assumptions about the strength of the relationships between prey abundance and demographic rates. Comparison made among the estimated relationships between prey abundance and demographic rates (middle line of projections for each set), 50% greater slopes for the relationships (upper value in each set), and 50% lower slopes (third value in each set).

	Threats modelled					**Population projections**		
Scenario	Chinook trend	Noise	PCB (ppm/y)	Oil spill (big; small)	Ship strikes	Population growth (r)	Probability extinct	Probability final N < 30
No anthropogenic threats	constant	0	0	0	0	0.023 0.015 0.006	0 0 0	0 0 0
Current threats	constant	85%	2	0	0	-0.006 -0.006 -0.006	1% 1% 1%	26% 25% 25%

Low increase	-25% in 100y	92.5%	2	0.21%; 1.08%	1 per 10y	-0.015 -0.014 -0.013	12% 13% 11%	69% 67% 61%
Higher increase	-50% in 100y	100%	2	0.42%; 2.16%	2 per 10y	-0.025 -0.023 -0.021	47% 43% 35%	94% 90% 85%
Cumulative Project impacts	constant	100%	2	0.21%; 1.08%	1 per 10y	-0.018 -0.016 -0.014	19% 17% 12%	82% 76% 67%

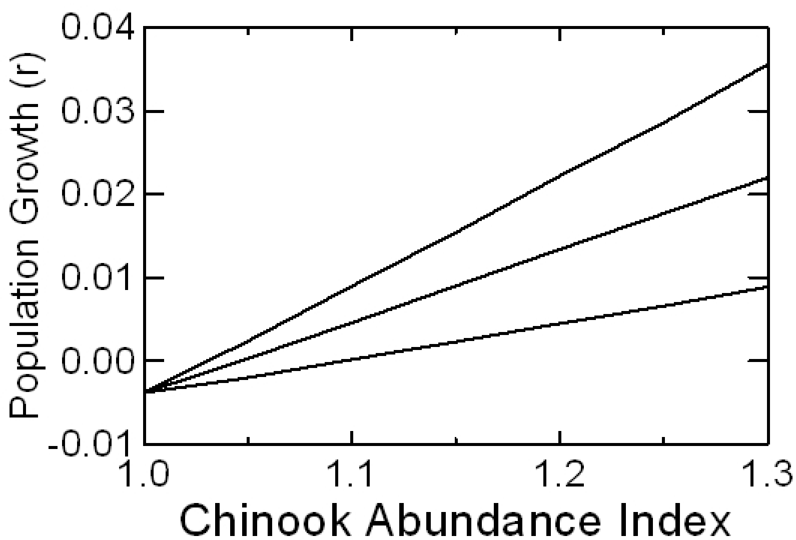

Figure 3. Mean population growth for SRKW achieved by increased Chinook prey abundance. Chinook abundance increased up to 1.3x the long-term mean. Middle line from projections with prey-demography relationships as estimated in prior models; top line from projections with the slope of the relationship increased 1.5x; bottom line from projections with the slope of the relationship decreased 0.5x.

Conclusions

Since the earlier analyses that were completed on data accumulated from 1976-2014, the SRKWs have experienced poorer reproduction and calf survival than the average over the past four decades of monitoring. This resulted in a decline to 74 killer whales in the population.

The observed recent decline is within the range that was projected in the prior models as possible annual variation – given the uncertainty in population processes (Figure 1). Thus, the most recent data do not give us any reason to reject the conclusions of the earlier analyses. However, continued refinement as more data become available, with constant monitoring for deteriorating or improving trends, would allow progressively more confidence in the model projections.

Although the recent decline might have been due simply to the random fluctuations in demographic events that occurs in wildlife populations, without any additional external cause, several aspects of the recent events could be cause for greater concern. Reproduction, for example, has been very low for the past three years, with no breeding in two of the three pods. In addition, the number of breeding age females has decreased by 6 since 2014, because recruitment of new mature females has not kept up with the loss of breeding potential as aging females become post-reproductive. Finally, in just 4 years, the mean age of the SRKWs that are not yet post-reproductive has increased from 19.3 to 20.3 years.

The projection based on currently available data is now that the population is, on average, in a slow decline, rather than the approximately stable population that was projected before the last four years of data were available (Table 1). The faster declines that are projected under various scenarios of Project impacts and Chinook declines are now expected to be worse than previously estimated, with the mean annual decline of 1.4% to 2.3% per year. These updated results indicate even greater urgency for actions that reverse existing threats, and avoid or fully mitigate any additional ones.

Our viability assessments clearly show that Southern Resident killer whales are already severely compromised as a result of living in an appreciably altered ecosystem where they are exposed to chronic disturbances and diminution of the life requisites upon which their survival depends (i.e. intact social systems, sufficient food, secure habitat, silent environment, and unimpeded movements). The number of boats on the water in the Salish Sea has increased dramatically in recent years and expected to continue to increase (DFO 2018). This escalation in traffic is disruptive to Killer Whales because more vessels are passing through their habitat and potentially disturbing how whales move through their environment. This is most evident when whales are interrupted from their normal activities in order to avoid a collision. Consequently, the Southern Residents are unable to effectively contend with the additional vessel traffic and related disturbances that would most likely result from the proposed Project.

As we have shown, the Southern Residents are imperiled and likely unsustainable without restoration of their primary prey of Chinook salmon, protection from noise and disturbance associated with current and expanding vessel traffic, and reduction of persistent pollutants that already compromise the immunity and reproductive capacity of the Southern Resident Killer whales. Reproductive failure (i.e. failure to produce viable offspring) and routine starvation of whales are manifestations of these cumulative human caused disturbances. Attempting to recover this already impaired population while subjecting it to additional harm from the proposed Project is destined to hasten the decline of this iconic and unique population of killer whales.

References

DFO. 2017. Southern Resident Killer Whale: A science based review of recovery actions for three at-risk whale populations. Available at: http://www.dfo-mpo.gc.ca/fm-gp/mammals-mammiferes/publications/whalereview-revuebaleine/review-revue/killerwhale-epaulard/index-eng.html [accessed February 2018].

Fisheries and Oceans Canada. 2018. Recovery Strategy for the Northern and Southern Resident Killer Whales (Orcinus orca) in Canada [Proposed]. Species at Risk Act Recovery Strategy Series, Fisheries & Oceans Canada, Ottawa, x + 84 pp.

Ford, M.J., K.M. Parsons, E.J. Ward, J.A. Hempelmann, C.K. Emmons, M. B. Hanson, K.C. Balcomb, L.K. Park. 2018. Inbreeding in an endangered killer whale population. Animal Conservation. doi:10.1111/acv.12413.

Lacy, R.C., K.C. Balcomb III, L.J.N. Brent, D.P. Croft, C.W. Clark, and P.C. Paquet. 2015. Report on Population Viability Analysis model investigations of threats to the Southern Resident Killer Whale population from Trans Mountain Expansion Project. Attachment E, Ecojustice – Written Evidence of Raincoast Conservation Foundation (A70286), National Energy Board (Canada). 120 pp. Available at http://docs.neb-one.gc.ca/fetch.asp?language=E&ID=A4L9G2.

Lacy, R. C., R. Williams, E. Ashe, K. C. Balcomb III, L. J. N. Brent, C. W. Clark, D. P. Croft, D. A. Giles, M. MacDuffee, and P. C. Paquet. 2017. Evaluating anthropogenic threats to endangered killer whales to inform effective recovery plans. Scientific Reports **7**:14119.

Appendix A

SCIENTIFIC REPORTS

OPEN

Evaluating anthropogenic threats to endangered killer whales to inform effective recovery plans

Received: 29 March 2017
Accepted: 11 October 2017
Published online: 26 October 2017

Robert C. Lacy[1], Rob Williams[2], Erin Ashe[2], Kenneth C. Balcomb III[3], Lauren J. N. Brent[4], Christopher W. Clark[5], Darren P. Croft[4], Deborah A. Giles[3], Misty MacDuffee[6] & Paul C. Paquet[6,7]

Understanding cumulative effects of multiple threats is key to guiding effective management to conserve endangered species. The critically endangered, Southern Resident killer whale population of the northeastern Pacific Ocean provides a data-rich case to explore anthropogenic threats on population viability. Primary threats include: limitation of preferred prey, Chinook salmon; anthropogenic noise and disturbance, which reduce foraging efficiency; and high levels of stored contaminants, including PCBs. We constructed a population viability analysis to explore possible demographic trajectories and the relative importance of anthropogenic stressors. The population is fragile, with no growth projected under current conditions, and decline expected if new or increased threats are imposed. Improvements in fecundity and calf survival are needed to reach a conservation objective of 2.3% annual population growth. Prey limitation is the most important factor affecting population growth. However, to meet recovery targets through prey management alone, Chinook abundance would have to be sustained near the highest levels since the 1970s. The most optimistic mitigation of noise and contaminants would make the difference between a declining and increasing population, but would be insufficient to reach recovery targets. Reducing acoustic disturbance by 50% combined with increasing Chinook by 15% would allow the population to reach 2.3% growth.

Conservation science is tasked with quantifying the relative importance of multiple anthropogenic threats to species, both to determine if cumulative impacts exceed sustainable levels and to guide effective recovery plans[1–4]. However, cumulative human impacts are often poorly understood and inadequately addressed in conservation and management[5]. Fundamental research is still needed to integrate information on qualitatively different stressors into comprehensive models that reveal the cumulative impacts on measures of population growth, stability, and resilience[6]. Such work is needed, in part, because threats vary widely in their amenity to mitigation. When regulators require users to forego economic opportunities, it is important to have confidence that management actions will achieve the desired effect[7]. One way to accomplish this is to conduct "population viability analyses" (PVA) that use models of population dynamics to evaluate the relative importance of multiple anthropogenic stressors, singly and in combination, so that conservation can be directed toward efforts most likely to promote species recovery[8]. PVA can be a powerful tool for informing management and conservation decisions. However, the detailed population models used in PVA depend on: availability of estimates for demographic rates (both fecundity and survival and the variability in such rates); confidence that observed past rates are predictors of ongoing demography, or that trends can be foreseen; data for quantifying effects of threats on demographic rates; and a population model that adequately captures the key demographic, social, genetic, and environmental processes that drive the dynamics of the population of concern. Nevertheless, even when data on certain aspects of the population or its threats are not available, we can use PVA models to explore possible outcomes across a plausible range of values, and thereby identify which factors might be important and the target of additional research.

The Southern Resident killer whale (*Orcinus orca*, SRKW) population in the northeastern Pacific Ocean is one of the most critically endangered populations of marine mammals in the USA[9] and Canada[10]. The USA and

[1]Chicago Zoological Society, Brookfield, IL 60513, USA. [2]Oceans Initiative, Seattle, WA 98102, USA. [3]Center for Whale Research, Friday Harbor, WA, 98250, USA. [4]College of Life & Environmental Sciences, University of Exeter, Exeter, Devon, EX4 4QG, UK. [5]Cornell Lab of Ornithology, Cornell University, Ithaca, NY, 14850, USA. [6]Raincoast Conservation Foundation, Sidney, BC V8L 3Y3, Canada. [7]University of Victoria, Victoria, BC V8P 5C2, Canada. Correspondence and requests for materials should be addressed to R.C.L. (email: rlacy@ix.netcom.com)

Set	Scenario	Parameters varied	Population growth (r)
Baseline	Baseline	Rates as observed 1976–2015	−0.002
	Sensitivity Tests	See Supplementary Information (S.I.)	See S.I.
Individual Threats	Current	Chinook = 1.0; Noise = 85%; PCB = 2 ppm/y	−0.001
	Chinook	0.6 to 1.3 × baseline	−0.038 to +0.025
	Noise	0 to 100% of time	+0.017 to −0.004
	PCB	0 to 5 ppm/y	+0.003 to −0.008
Cumulative Threats	No Anthropogenic Threats	baseline Chinook; no noise, no PCB; no oil spills; no ship strikes	+0.019
	Low Development	25% decline in Chinook; 92.5% noise; low frequency oil spills and ship strikes (see Table 2)	−0.008
	High Development	50% decline in Chinook; 100% noise; higher frequency oil spills and ship strikes (see Table 2)	−0.017
Demographic Management	Fecundity	1 to 1.5 × baseline	+0.016
	Adult Mortality	1 to 0.5 × baseline	+0.009
	Calf Mortality	1 to 0.5 × baseline	+0.004
Threat Management	Chinook	1 to 1.3 × baseline	+0.025
	Noise	85% to 0%	+0.017
	PCB	2 to 0 ppm/y	+0.004
	Chinook & Noise	1 to 1.3 × Chinook; 42.5% Noise	+0.036

Table 1. Models of viability of the SRKW population for assessing current viability, sensitivity to anthropogenic threats, and responses to management. Population growth rates are mean r for Baseline, ranges for tests of Individual Threats, means for Cumulative Threat scenarios, and maxima for ranges tested in Demographic Management and Threat Management scenarios.

Canada have listed this transboundary population as Endangered, citing three primary risk factors: lack of the whales' preferred prey, Chinook salmon (*Oncorhynchus tshawytscha*); chronic and acute underwater noise and physical disturbance (e.g., from ferries, commercial ships, whale-watching boats, fishing boats, and recreational traffic); and high levels of contaminants, including polychlorinated biphenyls (PCBs)[10,11]. A recent Status Review[12] highlighted also the potential risk to this small, localized population from catastrophic events such as an oil spill. Governments and non-governmental organizations are currently seeking effective conservation measures for this high-profile population. Fortunately, the biological and environmental data available for SRKWs are rich by the standards of any marine mammal population. Long-term annual censuses, with continuous monitoring since 1976, coupled with the specialized diet, have allowed inference of quantitative relationships between prey and various metrics of fecundity and survival[13,14]. Thus, the prerequisites for a robust PVA suitable for guiding conservation are met.

PVA uses demographic models to assess risk to wildlife populations and evaluate the likely efficacy of protection measures, recovery targets, and restoration options[15,16]. We used the Vortex PVA model to examine the dynamics of SRKWs. Vortex[17–19] is a flexible, individual-based simulation that is freely available. Vortex has been used to set recovery goals and guide actions for many threatened species, including the Mexican wolf (*Canis lupus baileyi*)[20], Florida panther (*Puma concolor coryi*)[21], and Florida manatee (*Trichechus manatus latirostris*)[22]. Several recent PVAs on the SRKWs have shown how variability in demography[23] or inter annual variability in Chinook salmon abundance[12,24,25] could affect the population. We extend those approaches to consider also the sub-lethal effects of contaminants and acoustic disturbance, and the cumulative impacts of threats and interactions among them.

We first parameterized a Baseline model with demographic rates observed over 1976 through 2014, and tested the sensitivity of population growth to each demographic parameter. We then constructed one model that quantifies the population consequences of all three anthropogenic threats to SRKWs identified in Canadian[10] and USA[11] recovery plans. We compared the relative importance of each threat by projecting the population growth across the possible range of each threat. Finally, we used the PVA to explore the degree to which threats would have to be mitigated, alone or in combination, to reach a quantitative USA recovery target of sustained 2.3% growth over 28 years[11].

Results

Five sets of population models and the scenarios examined in each are listed in Table 1. The Baseline model projects mean population growth over the next 100 years of $r = -0.002$, with variation across years of $SD = 0.045$ (Fig. 1). These projections match very closely to the rate of $r = 0.002$, with $SD = 0.042$, observed over 1976 to 2014. The marginally lower growth in the model can be accounted for by future accumulation of low levels of inbreeding. After 100 years, the projected mean inbreeding coefficient is 0.067, about the same as results from mating between first-cousins. When inbreeding depression was eliminated from the Baseline model, the projected growth was $r = 0.002$, with $SD = 0.043$ – nearly identical growth and variation in growth to the trend in recent decades, and thereby confirming that the model replicates accurately the recent dynamics of the population.

Sensitivity tests of the influence of each demographic rate in the baseline PVA (Supplementary Information) show that, across the ranges of values tested, variation in fecundity (defined for the model as the mean proportion of adult females giving birth per year) accounts for most (77%) of the uncertainty in population growth rate.

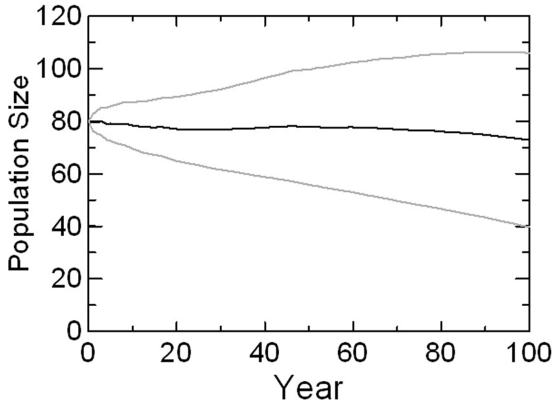

Figure 1. The distribution of 10,000 simulated trajectories with means and SD of the population size for northeastern Pacific Ocean SRKWs projected for 100 years, based on demographic rates observed from 1976 through 2014, applied to a starting population as it existed in 2015.

	Threats modelled					Population projection		
Scenario	Chinook trend	Noise	PCB (ppm/y)	Oil spill (big; small)	Ship strikes	Population growth (r)	Probability extinct	Probability final N < 30
No anthropogenic threats	constant	0	0	0	0	0.019	0	0
Current threats	constant	85%	2	0	0	−0.001	0	5%
Low increase	−25% in 100 y	92.5%	2	0.21%; 1.08%	1 per 10 y	−0.008	5%	31%
Higher increase	−50% in 100 y	100%	2	0.42%; 2.16%	2 per 10 y	−0.017	25%	70%

Table 2. Measures of viability of the SRKW population over 100 years under scenarios of minimal anthropogenic threats, current threats, and two levels of increased threats due to development. See text for explanation of threats modelled.

Annual adult mortality has some influence on the population trajectories (6%), but because mortality is already close to 0, there is comparatively less opportunity to improve the value of this parameter. Calf (first year) and juvenile (1 y to 10 y) mortality each accounted for about 3% of variation in population growth. Individual variation in reproductive success and temporal fluctuations (EV) in demographic rates had almost no effect on long-term population growth, as would be expected for a very long-lived species in which short-term fluctuations average out over time. Therefore, although our estimates of annual variation in rates are uncertain, refining the estimates would not change any conclusions about the effects of threats on the viability of the population. Given the small population size, inbreeding depression might cause sufficient adverse impact on population viability (6% of the total variance explained) such that it should not be ignored in assessments of long-term population viability. The impact of inbreeding was exacerbated slightly when we did not include avoidance of very close inbreeding (Supplemental Information).

Individual Threats. The set of models that includes estimates for the threats identified in the recovery plans – Chinook prey availability, noise and disturbance, and contaminants – was calibrated so that in the Current Threats scenario the demographic rates at existing threat levels reflect the mean demographic rates observed from 1976 through 2014. Thus, the Current Threats scenario mirrored the simpler Baseline scenario, except that rounding error in estimating effects of threats led to very slight deviation from the Baseline. The levels of these threats were then varied across broad ranges of values to determine which threat would have the greatest impact on population growth. Over the ranges tested, the effects of Chinook prey abundance on fecundity and survival had a greater effect on the population growth rate than did the other two factors (Fig. 2). Noise disturbance acts through decreased feeding efficiency in our model, but has a lesser effect than prey abundance because the maximum impact of boat noise 100% of the time would be to reduce foraging by about 20%. PCB accumulation rates that we tested result in mean levels in adult females of 0 to 132 ppm. Across this range, calf mortality is predicted to rise from about 7% to 50% (see Methods), and this impact shifts population growth from slightly positive to negative.

Cumulative Threats. Threats may interact, such that cumulative effects differ from those projected based on the summation of individual impacts. Full exploration of all of the possible interactions among the threats to the SRKW is not warranted at this time because individual threats are not yet well quantified. As more data on the above threats and other threats are acquired, management authorities can use the PVA framework to examine specific interactions of interest or full statistical analysis of all possible interactions[26]. To illustrate how cumulative threats can be assessed within the PVA model, we examined combinations of threat levels that represent the cumulative impacts of multiple threats for a few sample scenarios. We compared the Current Threats to a

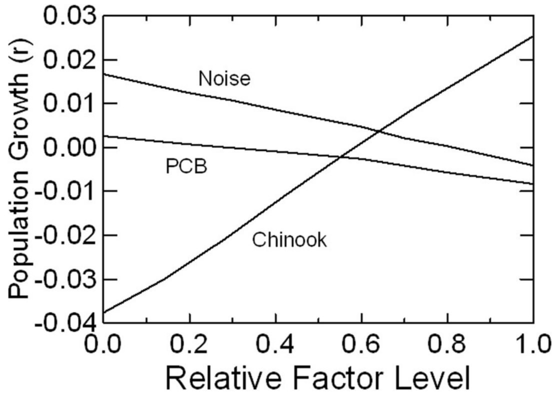

Figure 2. Effect of Chinook prey abundance (index varied from 0.60 to 1.30), noise and disturbance (boats present from 0% to 100% of time), and PCB contaminants (accumulation rate from 0 to 5 ppm/y) on mean population growth, while holding the other two factors at their baseline levels (1.0 prey index, 85% noise, and 2 ppm/y PCB accumulation). The x-axis is standardized to the range tested for each variable.

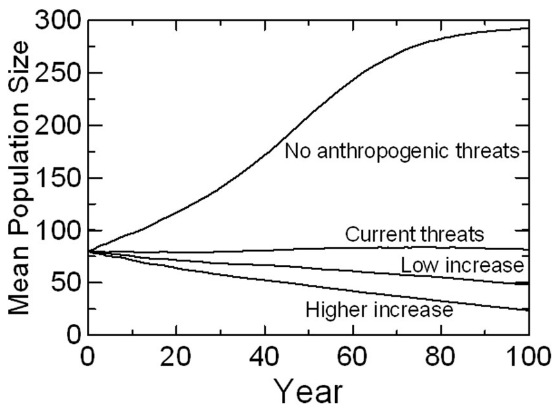

Figure 3. Mean projected SRKW population sizes for scenarios with (from top to bottom): no anthropogenic noise or contaminants; current Chinook abundance, noise, and PCBs; reduced Chinook, increased noise, and additional threats of oil spills and ship strikes as estimated for low level impacts of future industrial development; and these increased and additional threats with higher level impacts of development.

scenario with no anthropogenic threats and to scenarios with an increase in current threats and the addition of new threats. Figure 3 compares the population trajectory for the Current Threats with a scenario in which noise and PCB contamination were set to 0, and with two scenarios that describe levels of threat that could occur with proposed further industrial development and climate change. Table 2 shows the mean growth rates, probabilities of decline below 30 animals, and probabilities of extinction within 100 years under these scenarios.

The population could show robust growth if all anthropogenic threats were removed, but has no growth under current threat levels (Fig. 3). The combination of increased and additional threats expected under planned further industrial development in the habitat of the SRKW would cause population decline.

Demographic Management. The potential benefits of improvements in the primary demographic rates were examined in a set of Demographic Management scenarios. The demographic analyses indicate that reaching the SRKW recovery target of 2.3% growth is impossible by improving any single rate by a plausible amount, although increased fecundity would have the greatest positive influence on population growth (Fig. 4). To reach the recovery target, sustained mitigation of threats will be necessary to promote both increased fecundity and reduced mortality.

Threat Management. Improvements in demographic rates would need to be achieved by management actions that reduce threats or otherwise enhance the environment for SRKW. We therefore examined how population growth would respond to reductions in the levels of current threats. To achieve the recovery goal by increasing Chinook abundance alone would require a return to nearly the highest rates of Chinook abundance observed since 1979 (Fig. 5). If eliminating acoustic disturbance while maintaining current levels of Chinook abundance were possible, annual population growth could reach 1.7%. Removal of PCBs from the habitat would result in marginally positive (0.3%) growth, but the effect is much smaller than the impact of reduced noise and disturbance or increased Chinook abundance. Complete removal of both acoustic disturbance and PCBs is predicted to result in 1.9% growth. Therefore, reaching the recovery target without increasing Chinook salmon

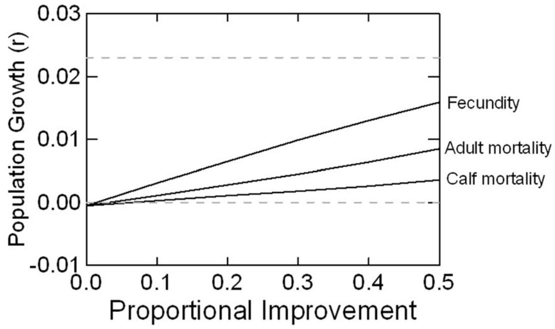

Figure 4. Mean population growth for SRKW achieved by improvements in demographic rates. Fecundity was increased from baseline to 1.5x baseline; mortality rates were decreased from baseline to 0.5x baseline. Dashed lines indicate a stated recovery target (2.3% growth) and r = 0.

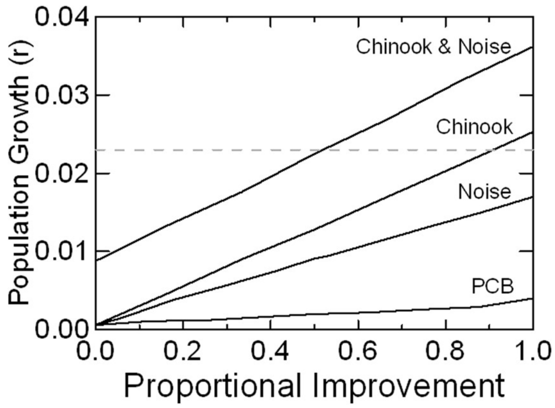

Figure 5. Mean population growth for SRKW achieved by mitigation of anthropogenic threats. Threat reductions are scaled on the x-axis from no reduction to the maximum reductions tested: Chinook abundance increased up to 1.3x the long-term mean; noise disturbance during feeding was reduced from 85% to 0; and PCBs were reduced from accumulation rates of 2 ppm/y to 0. The top line shows growth rates under a combination of varying levels of improved Chinook abundance plus mitigation of noise to half the current level.

numbers is likely impossible. Reducing acoustic disturbance by 50% and simultaneously increasing Chinook by more than 1.15x would allow the population to reach the 2.3% growth target. Other combinations of mitigation should be explored by management authorities as conservation options are identified.

Discussion

The SRKW population has experienced almost no population growth during the past four decades, and it declined in the last two decades. Intensive monitoring of the population since 1976 provides the information for construction of a detailed PVA model that closely replicates the observed population dynamics, and thereby provides a basis for projections under scenarios of increased anthropogenic threats or, conversely, increased mitigation actions. Models projecting population changes based on average demographic rates and fluctuations in those rates project that under the *status quo* the population will most likely remain near its current size. However, our use of baseline demographic rates averaged across 38 years of monitoring might give an overly optimistic projection for the SRKW if rates have deteriorated in recent years. A population projection based on demographic rates observed through 2011 projected a 1% annual mean growth[25], but a recent Status Review[12] projects a decline of 0.65% per year if demographic rates (such as recently lower fecundity) remain as they have been during 2011–2016. If ongoing monitoring indicates that these are not just short-term fluctuations in rates, then assessments of current viability, vulnerability to new or increased threats, and measures needed to achieve recovery will need to be revised.

When examined over ranges that encompass plausible improvements, the demographic parameter that presents the better opportunity for a large benefit to population growth is fecundity, rather than mortality. This finding is similar to a study of two bottlenose dolphin (*Tursiops aduncus*) populations off Australia, which found that variability in reproduction was more important than variability in mortality in driving differences between the populations[27]. There is simply more potential for improving reproduction than for improving adult survival when survival is already close to 1. Even complete elimination of adult mortality in the SRKW (not a biological possibility) would result in a population growth rate of 1.8%, still below the recovery goal of 2.3% growth. Although recovery cannot be achieved solely by improving adult survival, any decline in adult survival caused by new or exacerbated threats could have serious consequences for the population.

The PVA was useful for exploring scenarios representing the three main anthropogenic threats – prey limitation, acoustic and physical disturbance, and PCBs – that might worsen with increased development, or could be mitigated through management. Across the ranges of threat levels that we examined, reduction of the prey base was the single factor projected to have the largest effect on depressing population size and possibly leading to extinction, although either higher levels of noise and disturbance or higher levels of PCB contamination are sufficient to push the population from slow positive growth into decline. If additional threats from proposed and approved shipping developments (such as catastrophic and chronic oil spills, ship strikes, and increased vessel noise) combine with the predicted decline of Chinook due to climate change[28], then the population could decline by as much as 1.7% annually, have a 70% probability of declining to fewer than 30 animals, and have a 25% chance of complete extirpation within 100 years.

Mitigating multiple anthropogenic threats sufficiently to reach the recovery target will be difficult. The PVA is a useful way for managers to identify priorities for future research, and to focus conversations with ocean users and other special interests about the most pragmatic ways to promote recovery of endangered species. Those discussions must be integrated with considerations of feasibility, cost, societal impact, and timeframe for effective implementation. If a threat cannot be mitigated in a timescale relevant to conservation, or if costs are so high that they are prohibitive, thinking of those intractable problems as "fixed costs" in a cumulative impact management framework[4] might be useful. For example, our model results show that eliminating PCBs would provide less benefit to SRKWs than improving salmon returns or reducing anthropogenic noise and disturbance. This is fortuitous because imagining a way to eliminate PCBs that are persistent in the ecosystem is problematic[29], even though levels in tissues of SRKWs have been slowly declining in recent decades[30]. Identifying fixed costs that are difficult or impossible to mitigate allows a practical discussion about how to rank recovery actions among the anthropogenic factors that can be managed.

Of the three threats we considered, across wide but plausible ranges of each, salmon abundance is the greatest factor affecting SRKW population dynamics. Previously reported correlations of demographic rates with Chinook abundance[13,14,24] were used to parameterize our model, and Wasser *et al.*[31] recently offered insights into a mechanism that could cause the effect on fecundity: hormone levels indicate that SRKWs experience nutritional stress related to periods of lower abundance of Chinook prey and that this stress results in fewer successful pregnancies. Our PVA model estimated that SRKW recovery cannot be achieved without reaching the highest levels of salmon abundance observed since 1979, which was 30% higher Chinook salmon abundance than the long-term average between 1979 and 2008. This model result allows managers to focus discussions on whether achieving such a high sustained level of salmon abundance is attainable, and if so, how to achieve it. For example, removal of a hydroelectric dam on the Elwha River in the state of Washington is expected to increase spawning habitat for all five wild Pacific salmon species in the Salish Sea, but discussions about dam removal began in the 1960s[32] and the cost was in the hundreds of millions of US dollars. Restoration of spawning and rearing habitat could improve growth and survival of wild, juvenile salmon, but this takes political will, time, and money[33]. Improvement of marine survival of juvenile salmon might be possible by better management of net-pen salmon aquaculture sites that host and amplify viruses and parasites that have the potential to reduce survival of wild salmon[34,35]. Reducing Chinook harvest could provide an interim and strategic opportunity to rebuild depressed wild Chinook salmon runs and increase the number of Chinook available to whales in terminal areas like the Salish Sea[36]. Harvest reductions without longer term rebuilding plans might be an incomplete measure in places where Chinook harvests are already low due to abundance concerns or other constraints[37].

The SRKW population could be adversely affected by any new threats and further intensified impacts of the anthropogenic threats that we did assess. For example, pollutants other than PCBs might affect the population, and PCBs are known to have adverse effects beyond just reduced infant survival – such as reduced immune function[38]. However, other than calf survival, sufficient data are not yet available on the impacts of PCBs on demographic rates to allow incorporation of those threats in the population model. Moreover, threats to the population likely interact, perhaps in non-linear ways. For example, cetaceans that are food-limited might mobilize more lipids, and this will change the accumulated loads and harmful effects of PCBs and other organic pollutants. Similarly, reduction in foraging success because of boat noise might be of little consequence if prey is abundant, but could be critical if killer whales have difficulty procuring enough prey. If we can obtain data on additional threats and the interactions among threats, such effects could be included in the PVA models. At present, given that only estimates of approximate average effects of some threats are included in the model, inclusion of higher level interactions is premature.

While acknowledging that we examined only the identified primary threats to the SRKWs and that we cannot yet fully assess possible complex interactions among those threats, an important finding from our PVA is that reaching the recovery target will likely require mitigation of multiple threats. For example, the PVA projects that a 50% noise reduction plus a 15% increase in Chinook would allow the population to reach the 2.3% growth target. Noise is a particularly attractive issue to address in a management context, because it is amenable to several possible mitigation scenarios[39,40]. With respect to noise from commercial shipping, preliminary calculations suggest that the distribution of source levels of individual ships follows a power law, implying that quieting the noisiest ships will reduce overall noise levels by a disproportionate amount[41]. Identifying the noisiest ships operating in SRKW critical habitat[42] and creating incentives to reduce their noise outputs through speed restrictions and maintenance might generate considerable reductions in noise levels. The International Maritime Organization and the International Whaling Commission have urged nations to reduce the contribution of shipping to ocean ambient noise, with some countries adopting a pledge to reduce anthropogenic noise levels by 50% in the next decade[43]. However, from the perspective of a foraging killer whale that emits high-frequency (18-32 kHz) echolocation clicks to detect and capture salmon, high-frequency noise from small, outboard vessels that follow whales might cause a greater reduction in a killer whale's foraging success than low-frequency (<1 kHz) background noise from commercial shipping[44].

Clearly, even without new or increased external threats, the SRKW population has no scope to withstand additional pressures. The current situation for SRKWs gives little cause for optimism. This is likely to worsen, given the energy-related project proposals already approved for the region[45], which will increase broadband ocean noise levels and the risk of ship strikes and oil spills[46]. Our models of the additional threats expected with a proposed increase in oil shipping show that these threats will push a fragile population into steady decline. Obviously, countering such additional threats sufficiently to achieve SRKW population recovery would require even more aggressive mitigation actions than if there were no such increasing threats to the population.

The case study we present offers an unusual opportunity to examine multiple anthropogenic threats in a wildlife population that is extremely data-rich by the standard of any marine ecology study[5]. One threat (the impact of prey abundance through the prey-demography link) has been well studied for decades. Another (acoustic disturbance) is relatively well appreciated in that there are documented relationships between higher noise level and reduction in foraging success. However, a conceptual step is required to convert the reduction in foraging to a reduction in prey acquisition. Full consideration of noise impacts would need to include complex interactions among reduced foraging time, reduced detection space, and reductions in prey availability. The third kind of threat (population consequences of PCBs and other persistent pollutants) relies on very few data points to calibrate the effect of the PCBs only on whale calf survival, which underestimates the total population consequences of contaminants in two ways. Lack of concentration-response studies on compounds other than PCBs hinder our ability to model population consequences of PBDEs or other contaminants. Similarly, existing studies do not allow us to predict effects of contaminants on pregnancy rate or adult mortality. This spectrum of data-rich to data-poor steps in predicting population consequences of multiple stressors is ubiquitous in conservation and ecological studies[2,47]. The funding to fill knowledge gaps with empirical data may be lacking, or in the case of critically endangered species, time to wait for science to fill data gaps may be insufficient[48]. Some authors use expert elicitation[49,50] to fill data gaps. Expert opinion or examination of hypothetical, but plausible scenarios should be used to augment rather than replace the available data.

The case study presented here illustrates the use of PVA as a method to inform difficult conservation decisions, by simulating across plausible ranges of uncertainty. For example, sensitivity analyses revealed that some factors (e.g., individual variability in breeding success) have no effect, and such knowledge gaps should not be a barrier to management action. Given our inability to manage some insidious threats, such as persistent organic pollutants that are already in the environment, it is reassuring that the model predicts that this stressor has the smallest adverse impact on the population, at least via the pathway of reduced calf survival. The PVA can focus priority research on questions that make a practical difference. Studies of foraging efficiency under varying levels of anthropogenic disturbance are needed only because the population is prey-limited. If doubling Chinook salmon numbers were possible, and returning them to levels seen in the 1920s[51], consideration of other anthropogenic impacts on the whales' foraging efficiency might not be necessary. Alas, this is not a realistic scenario, and the model therefore points to the importance of including both improvement in prey abundance and reduction in noise as the more effective mitigation pathway.

Unfortunately, focus on only the immediate, tractable threats is all too common in conservation. For example, conservation of grizzly bears (*Ursus arctos horribilis*) in the continental United States focuses on roads and development activities, but the primary concern is that the species has been absent from most of its range since the 1800s[52]. Similarly, the current small size of the SRKW population was not caused by lack of salmon. The whales' depleted status is due in large part to the legacy of an unsustainable live-capture fishery for display in aquariums[53]. Salmon, noise, and contaminants are important factors that can prevent recovery. Many policies, including the US National Environmental Policy Act, require regulators to consider the effect of a proposed activity "which results from the incremental impact of the action when added to other past, present, and reasonably foreseeable future actions regardless of what agency (Federal or non-Federal) or person undertakes such other actions (40 CFR § 1508.7)." Allocating impacts among multiple ocean user sectors may be difficult, but in the case study we present, the population is sufficiently imperilled that it has little or no scope for tolerating additional stressors.

Methods

The SRKW population is closed to immigration and emigration, every individual in the population is known, and the population has been censused annually for decades[11]. Individuals were identified by their unique fin shapes, saddle patches, and the presence of any nicks or scratches, and sexed using distinctive pigmentation patterns around the genital slits. Male and female offspring remain within the natal, matrilineal unit, although mating occurs within and between these pods. The term "resident" refers to their residency in inshore waters of southern British Columbia (Canada) and Washington state (USA) in the summer months, when they feed almost exclusively on Chinook salmon[13,14,54,55]. Given that there is no dispersal from the population[56], mortality was recorded if an individual's matriline was observed in the population within a year but the individual did not appear.

We used values of demographic parameters calculated from the census data to build the population model in the Vortex PVA program[17,18]. We included temporal variation in demographic rates ("environmental variation"), based on inter-annual variability in parameters observed since 1976, and we included individual variation in age of maturity and probability of reproductive success. The Vortex simulation model of possible future population trajectories includes demographic stochasticity (binomial variation in individual fates); random assignment of sex and a bi-sexual mating system, resulting in fluctuations in sex ratio and mate availability that can affect small populations; and projections of loss of genetic diversity, allowing for inclusion of inbreeding depression. We quantified population growth as the mean exponential rate of increase ($r = \ln[N_{t+1}/N_t]$).

Modelling was conducted in stages. First, a "Baseline" model was developed to represent the population trajectories if demographic rates remain the same as have been observed in recent decades. We confirmed this Baseline model by comparing simulated dynamics with recent population trends. Secondly, we conducted sensitivity tests on uncertain demographic rates in the model to determine which parameters had large effects on the projected population growth. Thirdly, we used a set of models of Individual Threats that tested ranges of values for the primary threats identified in the recovery plans to determine which would have the greatest effects on population projections. Fourthly, we examined Cumulative Threats scenarios to project the fate of the population if further industrial development increases existing threats and adds new ones. A set of Demographic Management scenarios was then examined to determine the population growth that could be achieved by improvements in demographic rates. Finally, we explored Threat Management scenarios to assess the plausibility of reaching sustained annual population growth of 2.3% given various options for increasing salmon abundance, reducing ocean noise levels, or reducing contaminant levels. The following section describes key parameter estimates used in the model. More detailed description of the modelling methods is presented in Supplementary Information. The input files for the Vortex project are available at http://www.vortex10.org/SRKW.zip and from the Dryad Digital Repository at https://doi.org/10.5061/dryad.46vq7.

Baseline PVA. We started the simulations with the ages, sexes, and pod membership of the killer whales living in 2015. We specified the mother of each animal, where known (for 76 of 80 living animals)[57]. Based on previous genetic data on paternity[58], we specified in the simulation that females would not mate with their father, a son, or a maternal half-sibling. What effect lower levels of inbreeding or the inevitable accumulated inbreeding in a closed population will have on any cetacean is unknown. We modelled inbreeding depression as being caused by recessive lethal alleles, with 6.29 "lethal equivalents" (the negative of the slope of log(recruitment) against the inbreeding coefficient), the mean combined effect of inbreeding on fecundity and first-year survival in a survey of impacts on wild species[59].

Demographic rates were calculated from individual animal histories compiled by the Center for Whale Research[57], using data collected from 1976 through 2014. The time series begins when the population was depleted by live-captures for display in aquariums[60]. The time series therefore includes periods of moderate population growth (1976 to 1993), subsequent decline, and approximate stability. Demographic rates were estimated for the age-class groupings used in recent models[24,61], except that we set an upper limit for female breeding at 45 y rather than 50 y, because no females in the population have been documented to produce calves at older ages. Thus, we calculated survival and (for adult females) fecundity rates for calves (first year), juveniles (defined as from 1 y through 9 y of age), young mature females (10–30 y), older reproductive females (31–45 y), post-reproductive females (46 y and older), young mature males (10–21 y), and older males (22 y and older). Killer whales can survive many years after reproductive senescence, but estimating maximum longevity is difficult in such a long-lived species[62]. We set an upper limit of age to 90 y in our models, although only about 2% of females would be expected to reach this age, and only about 2% of males (with higher mortality) would be expected to exceed 50 y. Females stop breeding long before the maximum age, so the long-term population growth would not be affected by the upper age limit unless post-reproductive females benefit the pod in ways other than through their own reproduction.

Mortality for each age-sex class was averaged across the 39 years of data to obtain mean annual rates. We did not try to partition observed mortality into presumed causes of death. The use of these historic data for our Baseline model makes the implicit assumption that the frequency of deaths due to the various causes remains the same as has been observed across recent decades. The variation in mortality observed across years has two components: 1) environmental variation (fluctuations in the probability of survival), and 2) demographic stochasticity (binomial variation in individual fates). To determine how much of the observed variation was due to environmental variation, the variance due to demographic stochasticity can be calculated from the expectation for a binomial process, and then subtracted from the total variation across years. Calculated annual mortality rates (and environmental variation) ranged from a low of 0.97% (SD = 0) for young adult females to 17.48% (SD = 17.96) for calves. Although the lack of evidence for annual variation in the mortality adult females beyond that expected from random sampling of a constant probability might seem optimistic, for long-lived species a low level of annual variation in rates would have negligible effect on long-term population trajectories. We confirmed through sensitivity tests (Supplementary Information) that the environmental variation entered into the population model has no effect on our results.

The breeding system is polygamous, with some males able to obtain multiple mates, females mating with different males over their lifetimes, and mating between and within pods. Males become sexually mature (actively breeding, which may occur several years after they are physiologically capable of breeding) from 12 to 18 y of age. Thus, in the model, each male was assigned an age of sexual maturity by randomly selecting a value from 12 to 18. Variance in reproductive success among individual females and males will cause genetic diversity to be depleted faster and inbreeding to accumulate faster than would occur if mating was assumed random. Information is available on male mating success[51], and we incorporated variation in male and female reproductive success in the model (Supplementary Information). Our models project an effective population size that is 37% of the total size, close to an estimate obtained from genetic data[58].

Breeding rates, expressed as the proportion of the females of an age class that produce a calf each year, were calculated from annual census data. Rates ranged from 0% for post-reproductive females (age >45 y), to 7.88% (SD = 4.15) for older adult females (age 31–45 y), to 12.04% (SD = 3.54) for young adult females (age 10–30 y).

The upper limit on population size was set to 300, so that carrying capacity (K) would not restrict future population growth except under the best conditions tested. In the projections of current or expected conditions, the SRKW populations never reached this limiting size, and rarely exceeded 150 animals in any of the independent iterations of each simulation. Population recovery was assessed by the mean growth rate each year calculated before any carrying capacity truncation. Thus, the growth rate reflects the demographic potential and is not affected by the limit on population size in the model.

The SRKW population was projected for 100 years. For the initial exploration of parameter uncertainty, the simulation was repeated in 10,000 independent iterations to obtain high precision in mean and variance estimations. For comparisons among alternative management scenarios, less iteration is needed to obtain the relative influence of input values, and tests were run with 1,000 iterations. Sensitivity tests were conducted by varying each basic demographic rate (life table values for fecundity and mortality) over a range of ± 10% around the baseline value. For several model variables that describe other aspects of the population dynamics and are also very uncertain, a wider range of values was tested (see Supplementary Information).

Individual Threats. We explored the effects of three threats identified in the recovery strategies. For each of prey abundance, noise disturbance, and PCB contaminants, we scaled impacts such that the estimated current level of the threat resulted in the mean demographic rates reported over recent decades. Effects of prey limitation were modelled using published relationships linking inter-annual variability in Chinook salmon to inter-annual variability in calf and adult mortality[63] and fecundity[13,61]. A prey index was calculated by dividing the total salmon abundance in each year by its average abundance over the 1979–2008 period[63]. The relationship of mortality to prey abundance was modelled with a multiplier of baseline mortality that is a linear function scaled to 1 when salmon abundance was at the mean observed level over period of observation: MortalityFactor = 3.0412 – 2.0412 * PreyIndex. The relationship of birth rate to prey was modelled with logistic functions, with the intercept scaled to yield the observed birth rates for young females (12.04%) and older females (7.88%) when PreyIndex = 1. For relationships of form BirthRate = exp(A + B*PreyIndex)/[1 + exp(A + B*PreyIndex)], the function parameters were A = −3.0 and B = 1.0 for young females, and A = −3.46 and B = 1.0 for older females. (See Supplementary Information for more details on these relationships.) To explore the impacts of prey abundance across a range of plausible values, we varied the prey index from approximately the lowest level (0.60) reported since 1978 to approximately the highest level (1.30).

Effects of noise on demography were modelled using the approach outlined in previous analyses of loss of acoustic communication space[4,64]. We used summertime observations to estimate the proportion of time boats were present (during daylight hours) while the whales were foraging and the reduction in foraging expected with that amount of acoustic disturbance. We calibrated the model of noise impacts so that the mean Baseline demographic rates are obtained at the reported level of disturbance. We then simulated the relative change in foraging time and consequently demographic rates across the spectrum from no noise impact at all, to the upper limit expected if boat disturbance increased from current, already high, levels to 100% of time. We do not have data on the amount of acoustic disturbance in the winter feeding areas, but the modelling based on observed summertime disturbance provides a means to project a range of population consequences if changes in disturbance overall mirror those that are possible in the summertime habitat. Land-based observations have shown that SRKWs reduce their time spent feeding in the presence of boats by 25%[65]. Vessels are present 85% of the daytime, and SRKWs are foraging in the presence of vessels an estimated 78% of that time. Thus, for the 85% current (baseline) exposure to vessels, feeding is expected to be reduced by 16.6% (= 85% × 78% × 25%) due to disturbance by boats. To translate the reduction in feeding into its demographic consequences, we multiplied the prey index by a factor of (1 − 0.195 * Noise)/(1 – 0.166) to obtain the proportional availability of prey. This proportion is thus 1 in the current, baseline conditions (Noise = 0.85), 0.965 when vessels are always present (Noise = 1.00), and 1.20 assuming no disturbance from vessels. The noise-modified index of prey availability was then used to determine the consequent mortality and fecundity rates. We recognize that anthropogenic noise can also have less direct effects on wildlife, including disruption of social behaviours and even impeding responsiveness to other sensory modalities[66].

Our model of accumulation, depuration, and impact on calf survival of PCBs was based on the approach described by Hall *et al.*[67,68] with modifications in rates for SRKW[69]. Calves obtain their initial load of contaminants from their dams through gestation and lactation, and females producing calves thereby depurate an estimated 77% of their contaminants[67]. Otherwise, males and non-breeding females accumulate PCBs in the blubber of at a rate that we varied from 0 to 5 ppm/y in our tests. Few data are available on PCBs in the SRKW population with which to calibrate the model of PCB bioaccumulation, and the levels of PCBs reported in SRKW might have been dropping slowly in recent years. Reported levels in adult female SRKW range from 55 ± 19 ppm sampled in 1993–1996, 37 ± 42 ppm sampled in 2004–2007, and 30 ± 31 ppm sampled in 2008–2013[30]. Our population model generates a mean 28, 55, and 81 ppm PCBs in adult females when bioaccumulation rate is 1, 2, and 3 ppm/y, respectively. Effects of maternal PCB load on calf mortality were modelled using a logistic response function (survival = exp(2.65 − 0.02 * PCB)/[1 + exp(2.65 − 0.02 * PCB)]), fitted to the two observed data points for SRKW (survival = 0.8252) and the nearby northern resident killer whales (survival = 0.9218)[24], with the mean PCB levels (55.4 ppm and 9.3 ppm, respectively)[70] reported from the time period in the middle of the span over which mortality rates were calculated. If we use the more recent, lower estimates of PCB loads in SRKW to estimate the impacts, our response function would have a steeper slope. There are not yet sufficient data on effects of PCBs on other demographic rates to allow inclusion of any other effects of PCBs (or other contaminants) in our PVA model.

Cumulative Threats. We modelled two scenarios to represent the cumulative impacts of possible increases in threats, based in part on a recent environmental impact assessment submitted to Canada National Energy Board[45] evaluating effects of a proposed oil pipeline and associated tanker traffic. For the purposes of this PVA, projected increases in anthropogenic threats are not meant to mimic any one industrial development, but rather a general process of industrialization reflecting the number of port expansions, pipeline proposals, and liquefied natural gas terminal proposals pending for the BC coast[4]. For a low level scenario, we used the catastrophe option in Vortex to add the possibility of large (>16,500 m^3) and smaller (>8,250 m^3) oil spills. The frequencies of a big spill (0.21% chance per year) and a smaller spill (1.08%) were based on an industry projection of the likelihood of such spills caused by proposed increase in tanker traffic[71]. Based on the percent overlap of oil coverage and critical habitat, we estimate that if a large oil spill were to occur, about 50% of the SRKWs would be killed due to direct exposure to the oil. We estimate that 12.5% of the SRKWs would be killed by exposure to oil from a smaller spill. For a scenario with higher level impacts of development, we doubled the frequency of oil spills.

These energy development scenarios also included an increase in vessel noise and disturbance of feeding, with the current vessel presence of 85% of time increased to 92.5% in the low level scenario and to 100% in the high level scenario. We also included a probability of additional deaths of killer whales due to ship strikes, with one death per decade in the low level and two deaths per decade in the high level scenario. Although some persistent organic pollutants might increase under increased industrial activity in the SRKW habitat, PCBs have been phased out of production and are in decline in at least some fish species in low-development basins[72]. Lacking data on likely long-term trends in the contaminant loads of SRKW prey, we did not include any change in such pollutants in these scenarios.

Climate change is projected to cause a decline in Chinook abundance[28], and we modelled this possibility with a projected 25% (low scenario) or 50% (high scenario) decrease in Chinook over the next 100 years.

Demographic Management and Threat Management scenarios. We used the PVA to simulate how much improvement in demographic parameters or how much reduction in anthropogenic threats, singly or in combination, would be required to reach a stated recovery objective of sustained annual population growth of 2.3% for 28 years[11]. In calculating the growth for these models, we started the tally 20 years into the simulation to avoid short-term demographic fluctuations as the age structure adjusts to new demographic rates, and growth was tallied over the subsequent 28 years. For the set of Demographic Management scenarios, we assessed the relationship between improved demography and population growth. Birth rate was incremented by 1.1x, 1.2x, 1.3x, 1.4x, and 1.5x, whereas calf mortality and adult mortality were decreased by 0.9x, 0.8x, 0.7x, 0.6x, and 0.5x. Next, in Threat Management scenarios, we modelled the effects of reduced threats, with the consequences resulting from the functional relationships to demography. We increased salmon abundance (up to the highest level of the Chinook index observed between 1979 and 2008, namely 1.3 times the long-term average). We simulated the improved demography if acoustic disturbance were reduced or eliminated. We considered the population consequences of improved calf survival resulting from reduction of PCBs, testing rates of future accumulation in SRKW from the estimated current 2 ppm/y to down to 0 ppm/y. Finally, we tested scenarios that both reduced acoustic disturbance by half and increased salmon abundance up to 1.3x.

References

1. Wright, A. J. & Kyhn, L. A. Practical management of cumulative anthropogenic impacts with working marine examples. *Conserv. Biol.* **29**, 333–340 (2014).
2. Côté, I. M., Darling, E. S. & Brown, C. J. Interactions among ecosystem stressors and their importance in conservation. *Proc. Biol. Sci.* **283**, 20152592, https://doi.org/10.1098/rspb.2015.2592 (2016).
3. National Academy of Sciences. *Approaches to Understanding the Cumulative Effects of Stressors on Marine Mammals* (The National Academies Press, Washington, DC, 2016) https://doi.org/10.17226/23479.
4. Williams, R., Thomas, L., Ashe, E., Clark, C. W. & Hammond, P. S. Gauging allowable harm limits to cumulative, sub-lethal effects of human activities on wildlife: A case-study approach using two whale populations. *Mar. Policy* **70**, 58–64 (2016).
5. Maxwell, S. M. *et al*. Cumulative human impacts on marine predators. *Nat. Commun.* **4**, 2688, https://doi.org/10.1038/ncomms3688 (2013).
6. Lacy, R. C. *et al*. Metamodels for transdisciplinary analysis of population dynamics. *PLoS ONE* **8**, e84211, https://doi.org/10.1371/journal.pone.0084211 (2013).
7. Agardy, T., Di Sciara, G. N. & Christie, P. Mind the gap: addressing the shortcomings of marine protected areas through large scale marine spatial planning. *Mar. Policy* **35**, 226–232 (2011).
8. Boyce, M. S. Population viability analysis. *Annu. Rev. Ecol. Syst.* **23**, 481–506 (1992).
9. Reynolds, J. E. III, Marsh, H. & Ragen, T. J. Marine mammal conservation. *Endang. Species Res.* **7**, 23–28 (2009).
10. Fisheries and Oceans Canada. *Action Plan for the Northern and Southern Resident Killer Whale (Orcinus orca) in Canada*. Species at Risk Act Action Plan Series. (Fisheries and Oceans Canada, Ottawa, 2017).
11. National Marine Fisheries Service. *Recovery Plan for Southern Resident Killer Whales (Orcinus orca)* (National Marine Fisheries Service Northwest Region, Seattle, 2008).
12. National Marine Fisheries Service. *Southern Resident Killer Whales (Orcinus orca) 5-Year Review: Summary and Evaluation*. (National Marine Fisheries Service West Coast Region, Seattle, 2016) http://www.westcoast.fisheries.noaa.gov/publications/status_reviews/marine_mammals/kw-review-2016.pdf.
13. Ward, E. J., Holmes, E. E. & Balcomb, K. C. Quantifying the effects of prey abundance on killer whale reproduction. *J. Appl. Ecol.* **46**, 632–640 (2009).
14. Ford, J. K. B., Ellis, G. M., Olesiuk, P. F. & Balcomb, K. C. Linking killer whale survival and prey abundance: food limitation in the oceans' apex predator? *Biol. Lett.* **6**, 139–142 (2010).
15. Shaffer, M. L. Population viability analysis. *Conserv. Biol.* **4**, 39–40 (1990).
16. Beissinger, S.R. & McCullough, D.R. (eds). *Population Viability Analysis* (University of Chicago Press, Chicago, 2002).
17. Lacy, R. C. Structure of the VORTEX simulation model for population viability analysis. *Ecol. Bull.* **48**, 191–203 (2000).
18. Lacy, R.C. & Pollak, J.P. *Vortex: A Stochastic Simulation of the Extinction Process*. Version 10.0. (Chicago ZoologicalSociety, Brookfield, Illinois, 2014) www.vortex10.org/Vortex10.aspx.
19. Lacy, R.C., Miller, P.S. & Traylor-Holzer, K. *Vortex10 User's Manual* (IUCN SSC Conservation Breeding Specialist Group, and Chicago ZoologicalSociety, Apple Valley, Minnesota, 2014).
20. Carroll, C., Fredrickson, R. J. & Lacy, R. C. Developing metapopulation connectivity criteria from genetic and habitat data to recover the endangered Mexican wolf. *Conserv. Biol.* **28**, 76–86 (2014).
21. Maehr, D.S., Lacy, R.C., Land, E.D., Bass, O.L. Jr. & Hoctor, T.S. Evolution of population viability assessments for the Florida panther: a multiperspective approach. In *Population Viability Analysis* (eds. Beissinger, S. R. & McCullough, D.R.) 284–311 (University of Chicago Press, Chicago, 2002).
22. Marmontel, M., Humphrey, S. R. & O'Shea, T. J. Population viability analysis of the Florida manatee (*Trichechus manatus latirostris*), 1976–1991. *Conserv. Biol.* **11**, 467–481 (1997).

23. Krahn, M.M. *et al. 2004 Status review of Southern Resident killer whales (Orcinus orca) under the Endangered Species Act*. NOAA Tech. Memo. NMFSNWFSC-62 (U.S. Dept. Commerce, Washington, DC, 2013) https://www.nwfsc.noaa.gov/assets/25/6377_02102005_172234_krahnstatusrevtm62final.pdf.
24. Vélez-Espino, L. A. *et al*. Comparative demography and viability of northeastern Pacific resident killer whale populations at risk. *Canadian Technical Report of Fisheries and Aquatic Sciences* **2014**, 3084 (2014).
25. Ward, E.J. *et al*. Estimating the impacts of Chinook salmon abundance and prey removal by ocean fishing on Southern Resident killer whale population dynamics. NOAA Tech. Memo. NMFS-NWFSC-123. (U.S. Dept. Commerce, Washington, DC, https://www.nwfsc.noaa.gov/assets/25/4647_08132013_113012_ImpactsOnSRKWsTM123WebFinal.pdf 2013).
26. Prowse, T. A. A. *et al*. An efficient protocol for the sensitivity analysis of complex ecological models. *Ecosphere* **7**, e01238, https://doi.org/10.1002/ecs2.1238 (2016).
27. Manlik, O. *et al*. The relative importance of reproduction and survival for the conservation of two dolphin populations. *Ecol. Evol.* **6**, 3496–3512 (2016).
28. Muñoz, N. J., Farrell, A. P., Heath, J. W. & Neff, B. N. Adaptive potential of a Pacific salmon challenged by climate change. *Nat. Clim. Change* **5**, 163–166 (2014).
29. Hickie, B. E., Ross, P. S., Macdonald, R. W. & Ford, J. K. B. Killer whales (*Orcinus orca*) face protracted health risks associated with lifetime exposure to PCBs. *Environ. Sci. Technol.* **41**, 6613–6619 (2007).
30. Mongillo, T.M. *et al*. *Exposure to a Mixture of Toxic Chemicals: Implications for the Health of Endangered Southern Resident Killer Whales*. NOAA Tech. Memo. NMFS-NWFSC-135 (U.S. Dept. Commerce, Washington, DC, 2016) https://doi.org/10.7289/V5/TM-NWFSC-135.
31. Wasser, S. K. *et al*. Population growth is limited by nutritional impacts on pregnancy success in endangered Southern Resident killer whales (*Orcinus orca*). *PLoS One* **12**, e0179824 (2017).
32. Witze, A. Let the river run: Removing two dams from the Elwha is a can't-miss restoration experiment. *Science News* **187**, 22–26 (2015).
33. Sommer, T. R., Nobriga, M. L., Harrell, W. C., Batham, W. & Kimmerer, W. Floodplain rearing of juvenile Chinook salmon: evidence of enhanced growth and survival. *Can. J. Fish. Aquat. Sci.* **58**, 325–333 (2001).
34. Krkošek, M. *et al*. Declining wild salmon populations in relation to parasites from farm salmon. *Science* **318**, 1772–1775 (2007).
35. Miller, K. M. *et al*. Genomic signatures predict migration and spawning failure in wild Canadian salmon. *Science* **331**, 214–217 (2011).
36. Williams, R. *et al*. Competing conservation objectives for predators and prey: estimating killer whale prey requirements for Chinook salmon. *PLoS ONE* **6**, e26738, https://doi.org/10.1371/journal.pone.0026738 (2011).
37. Hilborn, R. *et al*. The Effects of Salmon Fisheries on Southern Resident Killer Whales: Final Report of the Independent Science Panel (ESSA Technologies, Vancouver, BC, 2012).
38. Desforges, J.-P. W. *et al*. Immunotoxic effects of environmental pollutants in marine mammals. *Environment International* **86**, 126–139 (2016).
39. Williams, R., Erbe, C., Ashe, E., Beerman, A. S. & Smith, J. C. Severity of killer whale behavioral responses to ship noise: A dose-response study. *Mar. Pollut. Bull.* **79**, 254–60 (2014).
40. Williams, R., Erbe, C., Ashe, E. & Clark, C. W. Quiet(er) marine protected areas. *Mar. Pollut. Bull.* **100**, 154–161 (2015).
41. Leaper, R. & Renilson, M.R. A review of practical methods for reducing underwater noise pollution from large commercial vessels. *Trans. RINA* **154** (A2) (2012).
42. Veirs, S., Veirs, V. & Wood, J. D. Ship noise in an urban estuary extends to frequencies used for echolocation by endangered killer whales. *PeerJ.* **4**, e1657, https://doi.org/10.7717/peerj.1657 (2016).
43. Malakoff, D. A push for quieter ships. *Science* **328**, 1502–1503 (2010).
44. Silber, G. K., Vanderlaan, A. S. M., Arceredillo, A. T. & Johnson, L. L. The role of the International Maritime Organization in reducing vessel threat to whales: process, options, action and effectiveness. *Mar. Policy* **36**, 1221–1233 (2012).
45. Canada National Energy Board. *National Energy Board Report. Trans Mountain Expansion Project* (National Energy Board, Calgary, Alberta,). https://docs.neb-one.gc.ca/ll-eng/llisapi.dll/2969681/National_Energy_Board_Report_-_OH-001-2014_-_A5A9H1.pdf 2016
46. Gaydos, J. K., Thixton, S. & Donatuto, J. Evaluating threats in multinational marine ecosystems: a Coast Salish First Nations and tribal perspective. *PLoS ONE* **10**, e0144861, https://doi.org/10.1371/journal.pone.0144861 (2015).
47. King, S. L., Schick, R. S. & Donovan, C. An interim framework for assessing the population consequences of disturbance. *Method. Ecol. Evol.* **6**, 1150–1158 (2015).
48. González-Suárez, M., Lucas, P. M. & Revilla, E. Biases in comparative analyses of extinction risk: mind the gap. *J. Anim. Ecol.* **81**, 1211–1222 (2012).
49. Donlan, C., Wingfield, D. K., Crowder, L. B. & Wilcox, C. Using expert opinion surveys to rank threats to endangered species: a case study with sea turtles. *Conserv. Biol.* **24**, 1586–1595 (2010).
50. Teck, S. J., Halpern, B. S. & Kappel, C. V. Using expert judgment to estimate marine ecosystem vulnerability in the California Current. *Ecol. Appl.* **20**, 1402–1416 (2010).
51. Irvine, J. R. & Fukuwaka, M. A. Pacific salmon abundance trends andclimate change. *ICES J. Mar. Sci.* **68**, 1122–1130 (2011).
52. Noss, R. F., Quigley, H. B., Hornocker, M. G., Merrill, T. & Paquet, P. C. Conservation biology and carnivore conservation in the Rocky Mountains. *Conserv. Biol.* **10**, 949–963 (1996).
53. Bigg, M. A. & Wolman, A. A. Live-capture killer whale (*Orcinus orca*) fishery, British Columbia and Washington, 1962-73. *J. Fish. Res. Board Can.* **32**, 1213–1221 (1975).
54. Hanson, M. B. *et al*. Species and stock identification of prey consumed by endangered southern resident killer whales in their summer range. *Endang. Species Res.* **11**, 69–82 (2010).
55. Ford, M. J. *et al*. Estimation of a killer whale (*Orcinus orca*) population's diet using sequencing analysis of DNA from feces. *PLoS ONE* **11**, e0144956, https://doi.org/10.1371/journal.pone.0144956 (2016).
56. Olesiuk, P. F., Bigg, M. A. & Ellis, G. M. Life history and population dynamics of resident killer whales (*Orcinus orca*) in coastal waters of British Columbia and Washington State. *Rep. Int. Whal. Comm.* **12**, 209–243 (1990).
57. Center for Whale Research. *Southern Resident Orca Survey. Review Copy. 20150320 update*. (Center for WhaleResearch, Friday Harbor, Washington, 2015).
58. Ford, M. J. *et al*. Inferred paternity and male reproductive success in a killer whale (*Orcinus orca*) population. *J. Hered.* **102**, 537–553 (2011).
59. O'Grady, J. J. *et al*. Realistic levels of inbreeding depression strongly affect extinction risk in wild populations. *Biol. Conserv.* **133**, 42–51 (2006).
60. Williams, R. & Lusseau, D. A killer whale social network is vulnerable to targeted removals. *Biol. Lett.* **2**, 497–500 (2006).
61. Vélez-Espino, L. A. *et al*. Relative importance of Chinook salmon abundance on resident killer whale population growth and viability. *Aquat. Conserv.* **25**, 756–780 (2015).
62. Ward, E. J., Parsons, K., Holmes, E. E., Balcomb, K. C. I. I. I. & Ford, J. K. B. The role of menopause and reproductive senescence in a long-lived social mammal. *Front. Zool.* **6**, 4, https://doi.org/10.1186/1742-9994-6-4 (2009).
63. Ford, J.K.B., Wright, B.M., Ellis, G.M., & Candy, J.R. Chinook Salmon Predation by Resident Killer Whales: Seasonal and Regional Selectivity, Stock Identity of Prey, and Consumption Rates. (Fisheries and Oceans Canada, Nanaimo BC, 2009).

64. Williams, R., Clark, C. W., Ponirakis, D. & Ashe, E. Acoustic quality of critical habitats for three threatened whale populations. *Anim. Conserv.* **17**, 174–185 (2014).
65. Lusseau, D., Bain, D. E., Williams, R. & Smith, J. C. Vessel traffic disrupts the foraging behavior of southern resident killer whales *Orcinus orca*. *Endang. Species Res.* **6**, 211–221 (2009).
66. Morris-Drake, A., Kern, J. M. & Radford, A. N. Cross-modal impacts of anthropogenic noise on information use. *Curr. Biol.* **26**, 2697–2840 (2016).
67. Hall, A. J. *et al*. Population consequences of polychlorinated biphenyl exposure in bottlenose dolphins – an individual based model approach. *Environ. Health Perspect.* **114**(Suppl. 1), 60–64 (2006).
68. Hall, A.J. *et al*. Assessing the population consequences of pollutant exposure to cetaceans using an individual based modelling framework. Tech. Rep. of International Whaling Commission, Tromsø, Norway, SC63–E5 (2011).
69. Hall, A.J. & Williams, R. The potential effect of PCBs on Killer whales – using the 'SPOC' individual based pollution model approach to estimate impacts on population growth. IWC SC meeting document SC/66a/E/2 (2015).
70. Ross, P. S., Ellis, G. M. & Ikonomou, M. G. High PCB concentrations in free-ranging Pacific killer whales, *Orcinus orca*: Effects of age, sex and dietary preference. *Mar. Pollut. Bull.* **40**, 504–515 (2000).
71. Det Norske Veritas (USA). *Termpol 3.15 – General Risk Analysis and Intended Methods of Reducing Risks. Trans Mountain Expansion Project*. https://apps.neb-one.gc.ca/REGDOCS/File/Download/2393696 and https://apps.neb-one.gc.ca/REGDOCS/File/Download/2393360 (2013).
72. West, J. E., O'Neill, S. M. & Ylitalo, G. M. Time trends of persistent organic pollutants in benthic and pelagic indicator fishes from Puget Sound, Washington, USA. *Arch. Environ. Contam. Toxicol.* **73**, 207–229 (2017).

Acknowledgements

We thank the team members for the Center for Whale Research for providing the complete databases of censuses and demographic trends from 1976 through 2014. We thank Ailsa Hall, Sea Mammal Research Unit, University of St. Andrews, for providing the model of bioaccumulation of PCBs in cetaceans.

Author Contributions

P.P. coordinated the project. K.C.B. and D.A.G. provide the core census and demographic database. R.W., E.A., L.J.N.B., C.W.C., D.P.C., P.P., and M.M. provided data on threats. R.C.L. built the population model and conducted the simulations. R.W., R.C.L. and P.P. led the writing. All authors contributed to and reviewed the manuscript.

Additional Information

Supplementary information accompanies this paper at https://doi.org/10.1038/s41598-017-14471-0.

Competing Interests: The authors declare that they have no competing interests.

Publisher's note: Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

ROBERT C. LACY

Conservation Science
Chicago Zoological Society
Brookfield, Illinois 60513 USA

Office phone: (708) 688-8432
email: Robert.Lacy@czs.org
http://www.vortex10.org

Home office:
192 Ocean View Road
Jonesboro, Maine, USA

Phone and FAX: (207)434-2710
email: rlacy@ix.netcom.com

Education

B.A., summa cum laude, Biology, Wesleyan University 1977
Secondary school teaching certification for general science and biology
M.A., Biology, Wesleyan University 1977
Thesis: Evolutionary strategies for temperature regulation in *Mus musculus*: A quantitative genetic approach
Ph.D., Evolutionary Biology (minors: Genetics, Ecology), Cornell University, August1982
Thesis: Population biology of mycophagous Drosophilidae in the eastern U.S.

Positions Held

1985 to present	Senior Conservation Scientist, Chicago Zoological Society
2003 to 2011	Chairman, IUCN Species Survival Commission (SSC) Conservation Breeding Specialist Group
1992 to 1993	Chairman, Dept. of Conservation Biology, Chicago Zoological Society
1982 to 1985	Assistant Professor of Biology, Franklin & Marshall College

Academic Appointments/Graduate Advisory Committees/Postdoctoral Advisees

1985 to present	Chicago Zoological Society, Department of Conservation Biology (Supervised 5 post-doctoral research associates.)
1991 to present	University of Chicago, Lecturer, Committee on Evolutionary Biology (Served on PhD advisory committees for 8 students.)
1999 to present	University of Illinois, Chicago, Adjunct Professor, Department of Biology (Served on PhD advisory committees for 4 students.)
various	External committee member for graduate students at University of Illinois-Urbana, Univ of Maryland, Univ of Wisconsin-Milwaukee, Macquarie Univ, Univ of New South Wales, Monash Univ, South Dakota State Univ, Univ Missouri-St Louis, Univ Montana, Purdue Univ, Otago Univ

Current Research Interests

Interaction among genetic, demographic, and environmental causes of extinction
Modeling the dynamics of linked systems affecting wildlife – including population biology, epidemiology, wildlife harvest, habitat fragmentation, and changes in human populations
Genetic management of captive populations

Inbreeding and outbreeding depression

Teaching Experience

Franklin and Marshall College
    Genetics, Vertebrate Biology, Biosocial and Environmental Problems
University of Chicago
    Conservation Biology graduate seminar
Chicago Zoological Society
    Lectures on evolution and conservation
Professional schools of the American Zoo and Aquarium Association
    Population Management (demography and genetics sections)
Advanced Training Program in the Conservation of Biodiversity
    Program coordination, lectures, and mentor for biologists from tropical countries
Escola Superior de Conservação Ambiental e Sustentabilidade (ESCAS, Brazil)
    Introduction to Conservation Decision-making
Numerous other workshops on genetic analysis and population management taught to wildlife biologists, zoo managers, and conservation biologists

Professional Societies

Association of Zoos and Aquariums
American Genetic Association
Society for Conservation Biology
Society for the Study of Evolution

Professional Service

Journal advisory boards: Zoo Biology, Conservation Genetics, International Zoo Yearbook
Species Conservation Strategic Planning Task Force, chair (2005-2008), IUCN SSC
Conservation Breeding Specialist Group, IUCN SSC (Chair, 2003-2011)
    Recent activities include advising US Fish and Wildlife Service, state wildlife agencies, wildlife agencies of other nations (Australia, Canada, Spain, Brazil, Kenya, Indonesia, Malaysia, India, Chile, Ecuador, South Africa) and international conservation organizations on the management of Florida panther, whooping crane, Sumatran rhinoceros, lion tamarins, lion-tailed macaque, black rhinoceros, Iberian lynx, Humboldt penguin, African penguin, grizzly bear, lowland tapir, and many other species.
Member of IUCN SSC Conservation Genetics Specialist Group
Member of AZA Small Population Management Advisory Group
Advisor to AZA Field Conservation Committee
Conservation Fellow, St Louis Zoo WildCare Institute

Honors and Grants

Peirce Award for Excellence in the Sciences, Wesleyan University, 1977

Phi Beta Kappa, 1976

Sigma Xi, 1978

Predoctoral Fellowship. NSF, 1977 - 1980.

Doctoral Dissertation - Research in Population Biology. NSF, 1979 - 1981, $4845.

Faculty research grants. Franklin & Marshall College, 1982 - 1985.

Studies of inbreeding depression in *Peromyscus* mice. Institute of Museum Services (IMS), 1985 - 1987, $22,775.

Electrophoretic analysis of zoo populations. IMS, 1986 - 1988, $24,995.

Studies of outbreeding depression in *Peromyscus* mice. IMS, 1987 - 1989, $25,000.

Electrophoretic analyses of endangered species. IMS, 1988 - 1990, $25,000.

Outstanding Service Awards, American Zoo and Aquarium Association, 1988, 1989, 2001, 2011

Chromosomal analysis of endangered species. IMS, 1989 - 1991, $101,347.

Predictability of inbreeding depression in insular and mainland populations. NSF, 1991-1994, $182,683.

Population Management 2000 software development. AZA Conservation Endowment Fund, 1999, $20,540.

Biocomplexity: Models and meta-networks for interdisciplinary research in biodiversity risk assessment. NSF, 2000-2002, $98,000 (with P Nyhus, F Westley, P Miller, and G Ness)

An experimental test of the effects of breeding strategies used in AZA conservation programs. AZA Conservation Endowment Fund, 2001, $42,926.

Experimental tests of the effects of captive breeding of wildlife. IMLS, 2002-2005, $75,000.

Pedigree reconstruction to sustain populations. IMLS, 2005-2007, $200,293 (with J. Dubach)

Meta-models as an approach to understanding biocomplexity. Private donor to Chicago Zoological Society, 2006-2010, $100,000.

President’s Award, Chicago Zoological Society, 2007.

IUCN Species Survival Commission Chair’s Citation of Excellence Award, 2008.

Linking behavioral types and animal "job performance" with population management in zoos. 2009 IMLS National Leadership Planning Grant, $22,535 (with J. Watters and D. Powell)

Incorporating mate choice into breeding recommendations. 2009 IMLS National Leadership Planning Grant, $48,997 (with C. Asa and K. Traylor-Holzer)

RCN: Using metamodels to enable transdisciplinary research for the study of dynamic biological systems under global change. NSF, 2012-2017, $490,905 (with H R Akcakaya, Stony Brook University).

George Rabb Award for Conservation Innovation, IUCN Species Survival Commission, 2012

Ulysses S Seal Award for Innovation in Conservation, IUCN Conservation Breeding Specialist Group, 2012

LCP NRDA Dolphin Assessment, sub-contract with Industrial Economics on contract from NOAA. 2014-2015. $118,000 (co-PI with R. Wells).

Building capacity in population modeling for species conservation. Chicago Board of Trade Endangered Species Fund, 2014, $3,000

Assessing conservation strategies for the Panamanian Golden frog. Chicago Board of Trade

Endangered Species Fund, 2014, $4,250

Species Conservation Toolkit Initiative, a partnership to design, develop, disseminate, and support software for species risk assessments and conservation planning. Funding from 15 institutions, 2015-2018, $500,000.

Impact of allowing mate choice on reproductive success and animal welfare. Association of Zoos & Aquariums, 2016-2017, $11,280 (with L. Miller, T. Snyder, C. Asa, and C. Kozlowski).

Presentations and international workshop participation in 2014

Course on Vortex 10 software, Chicago Zoological Society (instructor)

North American Congress on Conservation Biology, Missoula, MT. Presented paper on “How to consider genetic depletion and rescue within Population Viability Analyses”

Workshop on “PVA to Policy”, Longyearbyen, Norway. Presentation on “Linking models for integrated analysis of populations facing multiple, interacting threats”.

Symposium on “Assessing vulnerability of flora and fauna in polar areas”, Tromsø, Norway. Presented paper on “Linking PVA models to explore the impacts of declining polar ice on interconnected species in the arctic ecosystem”.

Workshop on “Molecular genetics for species management in zoos and aquaria”, Antwerp, Belgium. Presentation on “Some challenges in the use of molecular genetics in population management”

Workshop on “Adaptive management for species conservation along the captive-wild spectrum”, Melbourne, Australia.

Workshop on “Integrating models of animal social systems within PVA”, Blacksburg, VA.

CBSG Strategic Committee, New Delhi, India

CBSG Annual Meeting, New Delhi, India

Presentations and international workshop participation in 2015

Workshop on computer modeling of disease risk in amphibians, Smithsonian Tropical Research Institute, Panama (organizer and instructor)

Workshop on the use of epidemiological models for wildlife conservation, Auckland, New Zealand (organizer and instructor).

Workshop on the use of metamodels for species conservation assessments and planning, Sydney, Australia (organizer and instructor).

CBSG Strategic Committee, Al Ain, UAE

CBSG Annual Meeting, Al Ain, UAE

Presented paper and led session on “Species Conservation Toolkit Initiative”, Association of Zoos and Aquariums (AZA).

Working session, Small Population Management Advisory Group, AZA.

Workshop on the design on ZIMS (Zoological Information Management System) R3, Minneapolis.

Workshop on the effects of plague on the dynamics of prairie dogs and black-footed ferrets, National Black-footed Ferret Conservation Center.

Training on Outbreak model of infectious disease, Chicago Zoological Society (organizer and instructor).
Training on MetaModel Manager software for integrated conservation assessments, Chicago Zoological Society (organizer and instructor).

Presentations and international workshop participation in 2016

Invited presentation on "The what, why, who, where, and when of sustainabilities", Joint TAG Chairs Meeting, World Association of Zoos and Aquariums.
Led workshop on "Computer simulations aren't just for games!" King Scholars Program, Brookfield Zoo.
Led workshop on "Integrating molecular genetic data into pedigree analyses", Chicago Zoological Society.
Invited presentation on "Using Population Viability Analysis to explore impacts of noise on cetaceans", Scientific Committee, International Whaling Commission, Bled, Slovenia.
Workshop on assessing injury to bottlenose dolphins due to PCB contamination of an estuarine system, NOAA and Georgia Dept of Natural Resources, Atlanta, Georgia.
Invited plenary presentation on "Considering human impacts – if not yet the humans – in species risk assessments", IUCN SSC Conservation Breeding Specialist Group, Puebla, Mexico.
Led workshop on "MetaModels for interacting species (multi-species PVAs and conservation planning)", IUCN SSC Conservation Breeding Specialist Group, Puebla, Mexico.
Dept of Fisheries and Oceans Canada, presentation on "Predicting responses of St. Lawrence beluga to environmental change and anthropogenic threats to orient effective recovery actions".
University of Maine – Machias, invited talk on "Building tools for wildlife conservation".

Presentations and international workshop participation in 2017

Tools for managing island populations. Presented to New Zealand Department of Conservation.
One Plan Approach: Working together for species conservation. Presented at Latin America Zoo Association (ALZPA) annual conference. Havana, Cuba.
Training in advanced techniques for population modeling with Vortex. Presented at AZA Reproductive Management Center, St Louis, MO.
Overview of Species Conservation Toolkit Initiative. IUCN SSC Conservation Planning Specialist Group annual meeting, Berlin, Germany.
Outbreak software for modeling infectious disease. Presented at Disease Risk Assessment Workshop. IUCN Conservation Planning Specialist Group, Sao Paulo, Brazil.

Presentations and international workshop participation in 2017

Training in advanced techniques for population modeling with Vortex. Seattle, WA.

Publications (most are available for downloading from www.vortex10.org/lacypubs.html)

Lacy, R.C., C.B. Lynch and G.R. Lynch. 1978. Developmental and adult acclimation effects of ambient temperature on temperature regulation of mice selected for high and low levels of nest-building. Journal of Comparative Physiology B 123:185-192.

Lacy, R.C. 1978. Dynamics of t-alleles in *Mus musculus* populations: Review and speculation. The Biologist 60:41-67.
Lacy, R.C. 1979. The adaptiveness of a rare male mating advantage under heterosis. Behavior Genetics 9:51-54.
Lacy, R.C. and C.B. Lynch. 1979. Quantitative genetic analysis of temperature regulation in *Mus musculus*. I. Partitioning of variance. Genetics 91:743-753.
Lacy, R.C. 1980. The evolution of eusociality in termites: A haplodiploid analogy? American Naturalist 116:449-451.
Lacy, R.C. 1981. Taxonomic and distributional notes on some fungus-feeding North American *Drosophila* (Diptera, Drosophilidae). Entomological News 92:59-63.
Lacy, R.C. 1982. Niche breadth and abundance as determinants of genetic variation in populations of mycophagous drosophilid flies (Diptera:Drosophilidae). Evolution 36:1265-1275.
Lacy, R.C. 1983. Structure of genetic variation within and between populations of mycophagous *Drosophila*. Genetics 104:81-94.
Lacy, R.C. and P.W. Sherman. 1983. Kin recognition by phenotype matching. American Naturalist 121:489-512.
Lacy, R.C. 1984. Ecological and genetic responses to mycophagy in Drosophilidae (Diptera). Pages 286-301 in Q. Wheeler and M. Blackwell (eds.), Fungus/Insect Relationships: Perspectives in Ecology and Evolution. Columbia University Press, New York.
Lacy, R.C. 1984. Predictability, toxicity, and trophic niche breadth in fungus-feeding Drosophilidae (Diptera). Ecological Entomology 9:43-54.
Lacy, R.C. 1984. The evolution of termite eusociality: Reply to Leinaas. American Naturalist 123:876-878.
Hayssen, V. and R.C. Lacy. 1985. Basal metabolic rates in mammals: Taxonomic differences in the allometry of BMR and body mass. Comparative Biochemistry and Physiology 81A:741-754.
Hayssen, V., R.C. Lacy and P.J. Parker. 1985. Metatherian reproduction: Transitional or transcending? American Naturalist 126:617-632.
Lacy, R.C. 1985. Evidence that group selection counters the evolution of sexual dimorphism. Evolutionary Theory 7:173-177.
Lacy, R.C. 1985. Some genetic considerations for the management of captive populations suggested by computer simulations. AAZPA 1985 Annual Proceedings, 627-630.
Lacy, R.C. and C.E. Bock. 1986. The correlation of range size and local abundance of some North American birds. Ecology 67:258-260.
Lacy, R.C. 1987. Loss of genetic diversity from managed populations: Interacting effects of drift, mutation, immigration, selection, and population subdivision. Conservation Biology 1:143-158.
Lacy, R.C. 1987. Further genetic and demographic analyses of small rhino populations. Pachyderm (Newsletter of the African Elephant and Rhino Specialist Group) No. 9, pp. 16-19.
Lacy, R.C. 1988. A report on population genetics in conservation. Conservation Biology 2:245-247.

Lacy, R.C. 1988. Genetic variability in captive stocks: Assessing past loss, present status, and future outlook. AAZPA 1988 Annual Proceedings 113-121.

Lacy, R.C., M.L. Foster, and the Primate Department Staff. 1988. Determination of pedigrees and taxa of primates by protein electrophoresis. International Zoo Yearbook 27:159-168.

Lacy, R.C. 1988. Conservation genetics at Brookfield Zoo and the Brookfield-Melbourne genetics research programme. Bulletin of Zoo Management 26:27-29.

Lacy, R.C. and T.W. Clark. 1989. Genetic variability in black-footed ferret populations: Past, present, and future. Pages 83-103 in U.S. Seal, E.T. Thorne, M.A. Bogan, and S.H. Anderson (eds.), Conservation Biology and the Black-Footed Ferret. Yale University Press, New Haven.

Lacy, R.C. 1989. How many pairs are needed on the ark? Bison 4:24-28.

Lacy, R.C. 1989. Analysis of founder representation in pedigrees: Founder equivalents and founder genome equivalents. Zoo Biology 8:111-124.

Lacy, R.C, Flesness, N.R., and Seal, U.S. 1989. Puerto Rican parrot population viability analysis. Report to the U.S. Fish and Wildlife Service. IUCN SSC Captive Breeding Specialist Group, Apple Valley, Minnesota.

Seal, U.S. and R.C. Lacy. 1989. Florida panther population viability analysis. Report to the U.S. Fish and Wildlife Service. IUCN SSC Captive Breeding Specialist Group, Apple Valley, Minnesota.

Paine, F.L., J.D. Miller, G. Crawshaw, B. Johnson, R. Lacy, C.F. Smith III, and P.J. Tolson. 1990. Status of the Puerto Rican crested toad. International Zoo Yearbook 28:53-58.

Maguire, L.A. and R.C. Lacy. 1990. Allocating scarce resources for conservation of endangered subspecies: Partitioning zoo space for tigers. Conservation Biology 4:157-166.

Brewer, B.A., R.C. Lacy, M.L. Foster, and G. Alaks. 1990. Inbreeding depression in insular and central populations of *Peromyscus* mice. Journal of Heredity 81:257-266.

Maguire, L.A., R.C. Lacy, R.J. Begg, and T.W. Clark. 1990. An analysis of alternative strategies for recovering the eastern barred bandicoot in Victoria. Pages 147-164 in T.W. Clark and J.H. Seebeck (eds.), The Management and Conservation of Small Populations. Chicago Zoological Society, Brookfield, Illinois.

Lacy, R.C. and T.W. Clark. 1990. Population viability assessment of the eastern barred bandicoot in Victoria. Pages 131-146 in T.W. Clark and J.H. Seebeck (eds.), The Management and Conservation of Small Populations. Chicago Zoological Society.

George, G.G., J. Dixon, G. Challis, and R.C. Lacy. 1990. Taxonomy and palaeontology of the eastern barred bandicoot. Pages 33-46 in T.W. Clark and J.H. Seebeck (eds.), The Management and Conservation of Small Populations. Chicago Zoological Society.

Seal, U.S. and R.C. Lacy. 1990. Florida Key Deer (*Odocoileus virginianus clavium*) population viability assessment. Report to the U.S. Fish and Wildlife Service. IUCN SSC Captive Breeding Specialist Group, Apple Valley, Minnesota.

Lindenmayer, D.B., V.C. Thomas, R.C. Lacy, and T.W. Clark. 1991. Population Viability Analysis (PVA): The concept and its applications, with a case study of Leadbeater's Possum, *Gymnobelideus leadbeateri* McCoy. Report to the Forest and Timber Inquiry (Resource Assessment Commission), Consultancy Series No. FTC91/18, Canberra, Australia. 170 pp.

Clark, T.W., G.N. Backhouse, and R.C. Lacy. 1991. The population viability assessment workshop: A tool for threatened species management. Endangered Species Update 8:1-5.

Clark, T.W., G.N. Backhouse, and R.C. Lacy. 1991. Report of a workshop on population viability assessment as a tool for threatened species management and conservation. Australian Zoologist 27:28-35.

Lacy, R.C. 1991. Zoos and the surplus problem: An alternative solution. Zoo Biology 10:293-297.

Johnston, L.A. and R.C. Lacy. 1991. Utilization of sperm banks to maintain genetic diversity in captive populations of wild cattle. Pages 107-118 in D.L. Armstrong and T.S. Groves (eds.), Wild Cattle Symposium Proceedings. Henry Doorly Zoo, Omaha, Nebraska.

Seal, U.S., R.C. Lacy, K. Medley, R. Seal, and T.J. Foose. 1991. Tana River Primate Reserve Conservation Assessment Workshop Report. IUCN SSC Captive Breeding Specialist Group, Apple Valley, Minnesota.

Mirande, C., R. Lacy, and U. Seal. 1991. Whooping crane (*Grus americana*) conservation viability assessment workshop report. IUCN SSC Captive Breeding Specialist Group, Apple Valley, Minnesota.

Foose, T.J., R.C. Lacy, R. Brett, and U.S. Seal. 1991. Kenya black rhinoceros metapopulation workshop report. IUCN SSC Captive Breeding Specialist Group, Apple Valley, Minnesota.

Lacy, R.C. 1992. The effects of inbreeding on isolated populations: Are minimum viable population sizes predictable? Pages 277-296 in P.L. Fiedler and S.K. Jain (eds.), Conservation Biology: The Theory and Practice of Nature Conservation, Preservation and Management. Chapman and Hall, New York.

Lacy, R.C. and T. Kreeger. 1992. VORTEX Users Manual. A stochastic simulation of the extinction process. IUCN SSC Captive Breeding Specialist Group, Apple Valley, Minnesota.

Seal, U.S., R.C. Lacy, et al. 1992. Genetic management strategies and population viability of the Florida panther (*Felis concolor coryi*). Report to the U.S. Fish and Wildlife Service. IUCN SSC Captive Breeding Specialist Group, Apple Valley, Minnesota.

Ellis, S., K. Hughes, C. Kuehler, R. Lacy, and U. Seal. 1992. `Alala, Akohekohe, and Palila Population and Habitat Viability Assessment Reports. IUCN SSC Captive Breeding Specialist Group, Apple Valley, Minnesota.

Ellis, S., C. Kuehler, R. Lacy, K. Hughes, and U. Seal. 1992. Hawai`ian forest birds conservation assessment and management plan. IUCN SSC Captive Breeding Specialist Group, Apple Valley, Minnesota.

Lacy, R.C. 1993. Impacts of inbreeding in natural and captive populations of vertebrates: Implications for conservation. Perspectives in Biology and Medicine 36:480-496.

Lacy, R.C. 1993. VORTEX: A computer simulation model for Population Viability Analysis. Wildlife Research 20:45-65.

Lacy, R.C. 1993. GENES: A computer program for the analysis of pedigrees and genetic management of populations. Chicago Zoological Society, Brookfield, Illinois.

Lacy, R.C. and T.W. Clark. 1993. Simulation modeling of American marten populations: Vulnerability to extinction. Great Basin Naturalist 53:282-292.

Lacy, R.C., A.M. Petric, and M. Warneke. 1993. Inbreeding and outbreeding depression in captive populations of wild species. Pages 352-374 in N.W. Thornhill (ed.), The Natural History of Inbreeding and Outbreeding. University of Chicago Press.

Lindenmayer, D.B., R.C. Lacy, V.C. Thomas, and T.W. Clark. 1993. Predictions of the impacts of changes in population size and environmental variability on Leadbeater's Possum, *Gymnobelideus leadbeateri* McCoy (Marsupialia: Petauridae) using Population Viability Analysis: an application of the computer program VORTEX. Wildlife Research 20:67-86.

Lindenmayer, D.B., T.W. Clark, R.C. Lacy, and V.C. Thomas. 1993. Population viability analysis as a tool in wildlife conservation policy: With reference to Australia. Environmental Management 17:745-758.

Lindenmayer, D.B. and R.C. Lacy. 1993. Using a computer simulation package for PVA to model the dynamics of sub-divided populations: An example using hypothetical meta-populations of the mountain brushtail possum. International Congress on Modelling and Simulation. Proceedings. 2:615-620.

Lacy, R.C. 1993/1994. What is Population (and Habitat) Viability Analysis? Primate Conservation 14/15:27-33.

Lacy, R.C. 1994. Review of Hartl, G.B. and Markowski, J. (eds.) Ecological genetics in mammals. Journal of Mammalogy 75:1090-1093.

Jiménez, J.A., K.A. Hughes, G. Alaks, L. Graham, and R.C. Lacy. 1994. An experimental study of inbreeding depression in a natural habitat. Science 266:271-273.

Lacy, R.C. 1994. Managing genetic diversity in captive populations of animals. Pages 63-89 in M.L. Bowles and C.J. Whelan (eds.), Restoration and Recovery of Endangered Plants and Animals. Cambridge University Press, Cambridge.

Lacy, R.C. 1995. A sibling is as valuable as an offspring: Reply to Xia. American Naturalist 145:480-482.

Lindenmayer, D.B. and R.C. Lacy. 1995. Metapopulation viability of Leadbeater's Possum, *Gymnobelideus leadbeateri*, in fragmented old-growth forests. Ecological Applications 5:164-182.

Lindenmayer, D.B. and R.C. Lacy. 1995. Metapopulation viability of arboreal marsupials in fragmented old-growth forests: comparison among species. Ecological Applications 5:183-199.

Lacy, R.C., J.D. Ballou, F. Princée, A. Starfield, and E. Thompson. 1995. Pedigree analysis. Pages 57-75 in J.D. Ballou, M. Gilpin, and T.J. Foose (eds.), Population Management for Survival & Recovery. Analytical Methods and Strategies in Small Population Conservation. Columbia University Press, New York.

Ballou, J.D. and R.C. Lacy. 1995. Identifying genetically important individuals for management of genetic diversity in pedigreed populations. Pages 76-111 in J.D. Ballou, M. Gilpin, and T.J. Foose (eds.), Population Management for Survival & Recovery. Analytical Methods and Strategies in Small Population Conservation. Columbia University Press, New York.

Johnston, L.A. and R.C. Lacy. 1995. Genome resource banking for species conservation: Selection of sperm donors. Cryobiology 32:68-77.

Lacy, R.C. 1995. Culling surplus animals for population management. Pages 187-194 in

B.G. Norton, M. Hutchins, E.F. Stevens, and T.L. Maple (eds.) Ethics on the ark: Zoos, animal welfare, and wildlife conservation. Smithsonian Institution Press, Washington, DC.

Lindenmayer, D.B. and R.C. Lacy. 1995. A simulation study of the impacts of population subdivision on the mountain brushtail possum, *Trichosurus caninus* Ogilby (Phalangeridae: Marsupialia), in south-eastern Australia. I. Demographic stability and population persistence. Biological Conservation 73:119-129.

Lacy, R.C. and D.B. Lindenmayer. 1995. A simulation study of the impacts of population subdivision on the mountain brushtail possum, *Trichosurus caninus* Ogilby (Phalangeridae: Marsupialia), in south-eastern Australia. II. Loss of genetic variation within and between subpopulations. Biological Conservation 73:131-142.

Lindenmayer, D.B., M.A. Burgman, H.R. Akçakaya, R.C. Lacy, and H.P. Possingham. 1995. A review of the generic computer programs ALEX, RAMAS/space and VORTEX for modelling the viability of wildlife metapopulations. Ecological Modelling 82:161-174.

Lacy, R.C. 1995. Clarification of genetic terms and their use in the management of captive populations. Zoo Biology 14:565-577.

Lacy, R.C. 1995. Conservation geneticists make their case. (Book review.) Ecology 76:1684-1685.

Lacy, R.C., K.A. Hughes, and P.S. Miller. 1995. VORTEX Version 7 users manual. A stochastic simulation of the simulation process. IUCN/SSC Conservation Breeding Specialist Group. Apple Valley, Minnesota.

Altmann, J., S.C. Alberts, S.A. Haines, J. Dubach, P. Muruthi, T. Coote, E. Geffen, D.J. Cheesman, R.S. Mututua, S.N. Saiyalel, R.K. Wayne, R.C. Lacy, and M.W. Bruford. 1996. Behavior predicts genetic structure in a wild primate group. Proc. Nat. Acad. Sci. USA 93:5797-5801.

Lacy, R. 1996. Further population modelling of northern white rhinoceros under various management scenarios. Appendix 3 in T.J. Foose (ed.). Summary – Northern White Rhinoceros Conservation Strategy Workshop. International Rhino Foundation, Cumberland, Ohio.

Lacy, R.C. and B.E. Horner. 1996. Effects of inbreeding on skeletal development of *Rattus villosissimus*. Journal of Heredity 87:277-287.

Lacy, R.C., G. Alaks, and A. Walsh. 1996. Hierarchical analysis of inbreeding depression in *Peromyscus polionotus*. Evolution 50:2187-2200.

Hedrick, P.W., R.C. Lacy, F.W. Allendorf, and M.E. Soulé. 1996. Directions in conservation biology: Comments on Caughley. Conservation Biology 10:1312-1320.

Lacy, R.C. 1996. Review of J.C. Avise and J.L. Hamrick (eds.). Conservation Genetics: Case histories from nature. Quarterly Review of Biology 71:566.

Lacy, R.C. 1997. Importance of genetic variation to the viability of mammalian populations. Journal of Mammalogy 78:320-335.

Lacy, R.C. and B.E. Horner. 1997. Effects of inbreeding on reproduction and sex ratio of *Rattus villosissimus*. Journal of Mammalogy 78:877-887.

Ballou, J.D., R.C. Lacy, D. Kleiman, A. Rylands, and S. Ellis. 1998. Leontopithecus II.

The second Population and Habitat Viability Assessment for Lion Tamarins (*Leontopithecus*). IUCN/SSC Conservation Breeding Specialist Group, Apple Valley, MN.

Lindenmayer, D.B., R.C. Lacy, and K.L. Viggers. 1998. Modelling survival and capture probabilities of the mountain brushtail possum (*Trichosurus caninus*) in the forests of south-eastern Australia using trap-recapture data. Journal of Zoology 245:1-13.

Lacy, R.C. and J.D. Ballou. 1998. Effectiveness of selection in reducing the genetic load in populations of *Peromyscus polionotus* during generations of inbreeding. Evolution 52:900-909.

Miller, P.S. and R.C. Lacy. 1999. VORTEX Version 8 users manual. A stochastic simulation of the simulation process. IUCN/SSC Conservation Breeding Specialist Group. Apple Valley, Minnesota.

Brook, B.W., J.R. Cannon, R.C. Lacy, C. Mirande, and R. Frankham. 1999. Comparison of the population viability analysis packages GAPPS, INMAT, RAMAS and VORTEX for the whooping crane (*Grus americana*). Animal Conservation 2:23-31.

Araya, B., D. Garland, G. Espinoza, A. Sanhuesa, A. Simeone, A. Teare, C. Zavalaga, R. Lacy, and S. Ellis. (eds.) 1999. Taller Análisis de la Viabilidad del Hábitat y de la Población del Pinguino Humboldt (*Spheniscus humboldti*). Informe final. IUCN/SSC Conservation Breeding Specialist Group, Apple Valley, MN.

Cooper, J., D. Oschadleus, L. Shannon, M. Thornton, P. Whittington, R. Lacy, and S. Ellis (eds.) 1999. African Penguin Population and Habitat Viability Assessment. IUCN/SSC Conservation Breeding Specialist Group, Apple Valley, MN.

Lindenmayer, D.B., R.C. Lacy, H. Tyndale-Biscoe, A.C. Taylor, K.L. Viggers, and M.L. Pope. 1999. Integrating demographic and genetic studies of the Greater Glider *Petauroides volans* in fragmented forests: predicting movement patterns and rates for future testing. Pacific Conservation Biology 5:2-8.

Ellis, S., R.C. Lacy, S. Kennedy-Stoskopf, D.E. Wildt, J. Shillcox, O. Byers, and U.S. Seal. 1999. Florida panther population and habitat viability assessment and genetics workshop report. IUCN/SSC Conservation Breeding Specialist Group, Apple Valley, MN.

Lindenmayer, D.B., R.C. Lacy, and M.L. Pope. 2000. Testing a simulation model for Population Viability Analysis. Ecological Applications 10:580-597.

Lacy, R.C. 2000. Management of limited animal populations. Pages 75-93 in D. Duffield and T. Robeck (eds.). Bottlenose dolphin reproduction workshop. Report. AZA Marine Mammal Taxon Advisory Group, Silver Spring, MD.

Pergams, O.R.W., R.C. Lacy, and M.V. Ashley. 2000. Conservation and management of Anacapa Island Deer Mice. Conservation Biology 14:819-832.

Penn, A.M., W.B. Sherwin, G. Gordon, D. Lunney, A. Melzer, and R.C. Lacy. 2000. Demographic forecasting in koala conservation. Conservation Biology 14:629-638.

Lacy, R.C. 2000. Should we select genetic alleles in our conservation breeding programs? Zoo Biology 19:279-282.

Land, E.D., and R.C. Lacy. 2000. Introgression level achieved through Florida Panther genetic restoration. Endangered Species Update 17:100-105.

Lacy, R.C. 2000. Considering threats to the viability of small populations. Ecological Bulletins

48:39-51.
Lacy, R.C. 2000. Structure of the VORTEX simulation model for population viability analysis. Ecological Bulletins 48:191-203.
Pollak, J. P., R. C. Lacy and J. D. Ballou. 2000. Population Management 2000, version 1.175. Chicago Zoological Society, Brookfield, IL.
Lacy, R.C., and J.D. Ballou. 2001. Population Management 2000 User’s Manual. Chicago Zoological Society, Brookfield, IL.
Lindenmayer, D.B., and R.C. Lacy. 2002. Small mammals, habitat patches and PVA models: a field test of model predictive ability. Biological Conservation 103:247-265.
Lacy, R.C., and P.S. Miller. 2002. Incorporating human populations and activities into population viability analysis. Pages 490-510 in S.R. Beissinger and D.R. McCullough (eds.), Population Viability Analysis. University of Chicago Press, Chicago.
Maehr, D.S., R.C. Lacy, E.D. Land, O.L. Bass, and T.S. Hoctor. 2002. Evolution of Population Viability Assessments for the Florida panther: A multiperspective approach. Pages 284-311 in S.R. Beissinger and D.R. McCullough (eds.), Population Viability Analysis. University of Chicago Press, Chicago.
Hosack, D.A., P.S. Miller, J.J. Hervert, and R.C. Lacy. 2002. A population viability analysis for the endangered Sonoran pronghorn, *Antilocapra americana sonoriensis*. Mammalia 66:207-229.
Nyhus, P.J., F.R. Westley, R.C. Lacy, and P.S. Miller. 2002. A role for natural resource social science in biodiversity risk assessment. Society and Natural Resources 15:923-932.
Jones, K.L., T.C. Glenn, R.C. Lacy, J.R. Pierce, N. Unruh, C.M. Mirande, F. Chavez-Ramirez. 2002. Refining the whooping crane studbook by incorporating microsatellite DNA and leg banding analyses. Conservation Biology 16:789-799
Maehr, D.S., and R. C. Lacy. 2002. Avoiding the lurking pitfalls in Florida panther recovery. Wildlife Society Bulletin 30:971-978.
Ryan, K.K., R.C. Lacy, and S.W. Margulis. 2002. Impacts of inbreeding on components of reproductive success. Pages 82-96 in: W. V. Holt, A. R. Pickard, J. C. Rodger, and D. E. Wildt, eds. Reproductive Science and Integrated Conservation. Cambridge University Press, Cambridge, UK.
Ryan, K.K., and R.C. Lacy. 2003. Monogamous male mice bias behaviour towards females according to very small differences in kinship. Animal Behaviour 65: 379-384.
Lindenmayer, D. B., H. P. Possingham, R. C. Lacy, M. A. McCarthy and M. L. Pope. 2003. How accurate are population models? Lessons from landscape-scale tests in a fragmented system. Ecology Letters 6:41-47.
Miller, P.S., and R.C. Lacy. 2003. VORTEX: A Stochastic Simulation of the Extinction Process. Version 9 User’s Manual. Conservation Breeding Specialist Group (SSC/IUCN), Apple Valley, Minnesota.
Miller, P.S., and R.C. Lacy. 2003. Integrating the human dimension into endangered species risk assessment. Pages 41-63 in: F.R. Westley and P.S. Miller, eds. Experiments in Consilience: Integrating Social and Scientific Responses to Save Endangered Species. Island Press, Washington, DC.
Miller, P.S., and R.C. Lacy. 2003. Metamodels as a tool for risk assessment. Pages 333-351 in:

F.R. Westley and P.S. Miller, eds. Experiments in Consilience: Integrating Social and Scientific Responses to Save Endangered Species. Island Press, Washington, DC.

Westley, F., P.S. Miller, and R.C. Lacy. 2003. Far from land: Further explorations in consilience. Pages 352-361 in: F.R. Westley and P.S. Miller, eds. Experiments in Consilience: Integrating Social and Scientific Responses to Save Endangered Species. Island Press, Washington, DC.

Singleton, I., S. Wich, S. Husson, S. Stephens, S. Utami Atmoko, M. Leighton, N. Rosen, K. Traylor-Holzer, R. Lacy, and O. Byers (eds.). 2004. Orangutan Population and Habitat Viability Assessment: Final Report. IUCN/SSC Conservation Breeding Specialist Group, Apple Valley, MN.

Lacy, R.C., and A. Vargas. 2004. Informe sobre la gestión genética y demográfica del programa de cría para la conservación del lince ibérico: escenarios, conclusiones y recomendaciones. Ministerio de Medio Ambiente, Madrid, Spain.

Heinsohn, R., R. C. Lacy, D. B. Lindenmayer, H. Marsh, D. Kwan, and I.R. Lawler. 2004. Unsustainable harvest of dugongs in Torres Strait and Cape York (Australia) waters: two case studies using population viability analysis. Animal Conservation 7:417-425.

Lacy, R.C., M. Borbat, and J.P. Pollak. 2005. VORTEX: A Stochastic Simulation of the Extinction Process. Version 9.57. Chicago Zoological Society, Brookfield, Illinois, USA.

Margulis, S.W., M. Nabong, G. Alaks, A. Walsh, and R.C. Lacy. 2005. Effects of early experience on subsequent parental behaviour and reproductive success in oldfield mice, *Peromyscus polionotus*. Animal Behaviour 69:627-634.

Traylor-Holzer, K., R. Lacy, D. Reed, and O. Byers (eds.). 2005. Alabama Beach Mouse Population and Habitat Viability Assessment: Final Report. IUCN/SSC Conservation Breeding Specialist Group, Apple Valley, MN.

Mendelson, J.R. III, et al. (50 co-authors, including R.C. Lacy). 2006. Confronting amphibian declines and extinctions. Science 313:48.

Mendelson, J.R. III, et al. (18 co-authors, including R.C. Lacy). 2006. Responding to amphibian loss. Response. Science 314:1541-1542.

Matamoros, Y., H. Vargas, R. C. Lacy, O. Byers, E. Travis, G. Montoya. (Editores). 2006. Taller para Anàlisisde Viabilidad de Poblaciòny Hàbitatpara el Pingüino de Galápagos. Informe Final. Parque Nacional Galápagos, Puerto Ayora, Santa Cruz, Galápagos, Ecuador. 8-11 de febrero, 2005.

Zippel, K., R. Lacy, and O. Byers (eds.) 2006. *CBSG/WAZA Amphibian Ex Situ Conservation Planning Workshop Final Report.* IUCN/SSC Conservation Breeding Specialist Group, Apple Valley, MN.

Vargas, F.H., R.C. Lacy, P.J. Johnson, A. Steinfurth, R.J.M. Crawford, P.D. Boersma, and D.W. MacDonald. 2007. Modelling the effect of El Niño on the persistence of small populations: The Galápagos penguin as a case study. Biological Conservation 137:138-148.

Miller, P.S., F.R. Westley, A.P. Byers, and R.C. Lacy. 2007. An experiment in managing the human animal: The PHVA process and its role in conservation decision-making. Pages 173-188 in T.S. Stoinski, H.D. Steklis, and P.T. Mehlman. Conservation in the 21st century: Gorillas as a case study. Springer, New York.

Nyhus, P.J., R. Lacy, F.R. Westley, P.S. Miller, H. Vredenburg, P. Paquet, and J. Pollak. 2007. Tackling biocomplexity and meta-models for species risk assessment. Ecology & Society 12: 31 [online] URL: http://www.ecologyandsociety.org/vol12/iss1/art31/

Lacy, R.C. 2007. Understanding inbreeding depression: 20 years of experiments with *Peromyscus* mice. Pages 327-329 in F.W. Allendorf and G. Luikart. Conservation and the Genetics of Populations. Wiley-Blackwell, New York.

Pergams, O.R.W. and R.C. Lacy. 2008. Rapid morphological and genetic change in Chicago-area *Peromyscus*. Molecular Ecology 17:450-463.

Dasmahapatra, K.K., R.C. Lacy, and W. Amos. 2008. Estimating levels of inbreeding using AFLP markers. Heredity 100:286-295.

Wich, S.A., E. Meijaard, A.J. Marshall, S. Husson, M. Ancrenaz, R.C. Lacy, C.P. van Schaik, J. Sugardjito, T. Simorangkir, K. Traylor-Holzer, B.M.F. Galdikas, M. Doughty, J. Supriatna, R. Dennis, M. Gumal, C.D. Knott, and I. Singleton. 2008. Distribution and conservation status of the orang-utan (*Pongo* spp.) on Borneo and Sumatra: How many remain? Oryx 42:329-339.

Rudnick, J.A., and R.C. Lacy. 2008. The impact of assumptions about founder relationships on the effectiveness of captive breeding strategies. Conservation Genetics 9:1439-1450.

Lacy, R.C. 2008. Conservation breeding – a global view. Pages 381-398 in B.R. Sharma, N. Akhtar, B.K. Gupta (eds.). India's Conservation Breeding Initiative, Central Zoo Authority, New Delhi.

Lacy, R.C. 2008. Conservation breeding – challenges and protocols. Pages 263-289 in B.R. Sharma, N. Akhtar, B.K. Gupta (eds.). India's Conservation Breeding Initiative, Central Zoo Authority, New Delhi.

IUCN/SSC. 2008. Strategic Planning for Species Conservation: A Handbook. Version 1.0. Gland, Switzerland: IUCN Species Survival Commission. 104pp. (R Lacy was one of the writers and co-editors, and chaired the task force that developed the handbook.)

Lacy, R.C. 2009. Stopping evolution: Genetic management of captive populations. Pages 58-81 in: G. Amato, R. DeSalle, O.A. Ryder, and H.C. Rosenbaum. Conservation genetics in the age of genomics. Columbia University Press, New York.

Lacy, R.C. and R. Wells. 2009. Population Viability Analysis (PVA). Pages 25-29 in R.R. Reeves, and R.L. Brownell, Jr., eds. Indo-Pacific bottlenose dolphin assessment workshop report: Solomon Islands case study of *Tursiops aduncus. Occasional Paper of the Species Survival Commission*, No. 40, IUCN, Gland, Switzerland. 53 pp.

Marshall, A.J., R. Lacy, M. Ancrenaz, O. Byers, S.J. Husson, M. Leighton, E. Meijaard, N. Rosen, I. Singleton, S. Stephens, K. Traylor-Holzer, S.S.U. Atmoko, C.P. van Schaik, and S.A. Wich. 2009. Orangutan population biology, life history, and conservation. Pages 311-326 in: S.A. Wich, S.S.I. Atmoko, T.M. Setia, and C.P. van Schaik, eds. Orangutans. Oxford University Press, Oxford, UK.

Ivy, J.A., A, Miller, R.C. Lacy, and J. A. DeWoody. 2009. Methods and prospects for using molecular data in captive breeding programs: an empirical example using parma wallabies (*Macropus parma*). Journal of Heredity 100:441-454.

Leus, K., and R.C. Lacy. 2009. Genetic and demographic management of conservation

breeding programs oriented towards reintroduction. Pages 74-84 in: A. Vargas, C. Breitenmoser, and U. Breitenmoser (eds.) Iberian Lynx *Ex Situ* Conservation: An Interdisciplinary Approach. Fundación Biodiversidad / IUCN Cat Specialist Group, Madrid.

Ivy, J.A., and R.C. Lacy. 2010. Using molecular methods to improve the genetic management of captive breeding programs for threatened species. Pages 267-295 in: J.A. DeWoody, J.W. Bickham, C.H. Michler, K.M. Nicols, O.E. Rhodes, and K.E. Woeste, eds. Molecular Approaches in Natural Resource Conservation and Management. Cambridge University Press, Cambridge.

Malo, A.F., F. Martinez-Pastor, G. Alaks, J. Dubach, and R.C. Lacy. 2010. Effects of genetic captive-breeding protocols on sperm quality and fertility in the white-footed mouse. Biology of Reproduction 83:540-548.

Ballou, J.D., R.C. Lacy, and J.P. Pollak. 2010. PMx: software for demographic and genetic analysis and management of pedigreed populations. Chicago Zoological Society, Brookfield, Illinois, USA.

Lacy, R.C. 2011. Re-thinking *ex situ* vs. *in situ* species conservation. Pages 25-29 in: G. Dick, ed. Biodiversity is Life. Proceedings of the 65th Annual Conference of the World Association of Zoos and Aquariums. WAZA, Gland, Switzerland.

Asa, C.S., K. Traylor-Holzer, and R.C. Lacy. 2011. Can conservation-breeding programmes be improved by incorporating mate choice? International Zoo Yearbook 45:203-212.

Leus, K., K. Traylor-Holzer, and R.C. Lacy. 2011. Genetic and demographic population management in zoos and aquariums: recent developments, future challenges and opportunities for scientific research. International Zoo Yearbook 45:213-225.

Asa, C.S., K. Traylor-Holzer, and R.C. Lacy. 2011. Mate choice as a potential tool to increase population sustainability. WAZA Magazine 12: 23-25.

Baker, A.M., R.C. Lacy, K. Leus, and K. Traylor-Holzer. 2011. Intensive management of populations for conservation. WAZA Magazine 12: 40-43.

Frankham, R., J.D. Ballou, M.D. Eldridge, R.C. Lacy, K. Ralls, M.R. Dudash, and C.R. Fenster. 2011. Predicting the probability of outbreeding depression: critical information for managing fragmented populations. Conservation Biology 25:465-475.

Jamieson, I.G., and R.C. Lacy. 2012. Managing genetic issues in reintroduction biology. Pages 441-475 in: J.G. Ewen, D.P. Armstrong, K.A. Parker, & P.J. Seddon, eds. Reintroduction Biology: Integrating Science and Management. Wiley-Blackwell, Oxford, UK.

Lacy, R.C., J.D. Ballou, & J.P. Pollak. 2012. PMx: Software package for demographic and genetic analysis and management of pedigreed populations. Methods in Ecology & Evolution 3:433-437.

Bradshaw, C.J.A., C.R. McMahon, P.S. Miller, R.C. Lacy, M.J. Watts, M.L. Verant, J.P. Pollak, D.A. Fordham, T.A.A. Prowse, and B.W. Brook. 2012. Novel coupling of individual-based epidemiological and demographic models predicts realistic dynamics of tuberculosis in alien buffalo. Journal of Applied Ecology 49:268-277.

Ivy, J.A., and R.C. Lacy. 2012. A comparison of strategies for selecting breeding pairs to maximize genetic diversity retention in managed populations. Journal of Heredity 103:186-196.

Lacy, R.C. 2012. Extending pedigree analysis for uncertain parentage and diverse breeding systems. Journal of Heredity 103:197-205.

Lacy, R.C., and C. A. Beuchat. 2012. Managing the genetic health of the Basenji. The Basenji May/June 2012:10-13.

Desbiez, A., K. Traylor-Holzer, R. Lacy, et al. 2012. Population Viability Analysis of jaguar populations in Brazil. In: Jaguar in Brazil. CATnews (Special Issue) 7:35-37.

Frankham, R., J.D. Ballou, M.R. Dudash, M.D.B. Eldridge, C.B. Fenster, R.C. Lacy, J.R. Mendelson III, I.J. Porton, K. Ralls, and O.A. Ryder. 2012. Implications of different species concepts for conserving biodiversity. Biological Conservation 153:25-31.

Lacy, R.C., J.P. Pollak, P.S. Miller, L. Hungerford, and P. Bright. 2012. Outbreak version2.0. IUCN SSC Conservation Breeding Specialist Group. Apple Valley, MN, USA.

Lacy, R.C. 2013. Understanding inbreeding depression: 25 years of experiments with *Peromyscus* mice. Pages 491-492 in F.W. Allendorf, G. Luikart, and S.N. Aiken. Conservation and the genetics of populations. 2nd ed. John Wiley & Sons, Oxford, UK.

Lacy, R.C. 2013. Achieving true sustainability of zoo populations. Zoo Biology 32:19-26.

Lacy, R.C. and G. Alaks. 2013. Effects of inbreeding on skeletal size and fluctuating asymmetry of *Peromyscus polionotus* mice. Zoo Biology 32:125-133.

Prowse, T.A.A., C.N. Johnson, R.C. Lacy, C.J.A. Bradshaw, J.P. Pollak, M.J. Watts, and B.W. Brook. 2013. No need for disease: testing extinction hypotheses for the thylacine using multi-species metamodels. Journal of Animal Ecology 82:355-364.

Meile, R., R.C. Lacy, F.H. Vargas, and P.G. Parker. 2013. Modeling the potential effects of *Plasmodium* infection on the Galapagos penguin (*Spheniscus mendiculu*s). Auk 130: 440-448.

Lacy, R.C., K. Traylor-Holzer, and J.D. Ballou. 2013. Managing for true sustainability of species. WAZA Magazine 14:10-14.

Lacy, R.C., G. Alaks, and A. Walsh. 2013. Evolution of *Peromyscus leucopus* mice in response to a captive environment. PLoS ONE 8(8): e72452. doi:10.1371/journal.pone.0072452.

Lacy, R.C., P.S. Miller, P.J. Nyhus, J.P Pollak, B.E. Raboy, and S. Zeigler. 2013. Metamodels for transdisciplinary analysis of population dynamics. PLoS ONE 8(12): e84211. doi:10.1371/journal.pone.0084211.

Pollak, J.P., R.C. Lacy. 2013. MetaModel Manager. Version 1.0. Chicago Zoological Society, Brookfield, Illinois. Available: http://www.vortex10.org/MeMoMa.aspx.

Byers, O., and R.C. Lacy. 2014. From captivity to conservation: Conservation Breeding Specialist Group and the evolving role of zoos. Pages 107-111 in G. McGregor-Reid and G. Moore, eds. History of Zoos and Aquariums: From Royal Gifts to Biodiversity Conservation. North of England Zoological Society, Chester.

Carroll, C., R.J. Frederickson, and R.C. Lacy. 2014. Developing metapopulation connectivity criteria from genetic and habitat data to recover the endangered Mexican wolf. Conservation Biology 28:76-86.

Frankham, R., R.C. Lacy, J.D. Ballou, M.R. Dudash, M.D.B. Eldridge, C.B. Fenster, J.R. Mendelson III, I.J. Porton, K. Ralls, and O.A. Ryder. 2014. Species concepts for conservation: Reply to Russello and Amato. Biological Conservation 170:334-335.

Lacy, R.C., and J.P. Pollak. 2014. VORTEX: A Stochastic Simulation of the Extinction Process. Version 10.0. Chicago Zoological Society, Brookfield, Illinois, USA.

Lacy, R.C., P.S. Miller, and K. Traylor-Holzer. 2014. Vortex 10 User's Manual. IUCN SSC Conservation Breeding Specialist Group, and Chicago Zoological Society, Apple Valley, Minnesota, USA.

Lacy, R.C., J.P. Pollak, P.S. Miller, L. Hungerford, and P. Bright. 2014. Outbreak version 2.1. IUCN SSC Conservation Breeding Specialist Group. Apple Valley, Minnesota, USA.

Shoemaker, K.T., R.C. Lacy, M.L. Verant, B.W. Brook, T.M. Liveri, P.S. Miller, D.A. Fordham, and H.R. Akcakaya. 2014. Effects of prey metapopulation structure on the viability of black-footed ferrets in plague-impacted landscapes: a metamodelling approach. Journal of Applied Ecology 51:735-745.

Hoffman, J.I., F. Simpson, P. David, J.M. Rijks, T. Kuiken, M.A.S. Thorne, R.C. Lacy, K.K. Dasmahapatra. 2014. High-throughput sequencing reveals inbreeding depression in a natural population. Proceedings of the National Academy of Sciences 111:3775-3780.

Hedrick, P.W., and R.C. Lacy. 2015. Measuring relatedness between inbred individuals. Journal of Heredity 106:20-25.

Willoughby, J.R., N.B. Fernandez, M.C. Lamb, J.A. Ivy, R.C. Lacy, and J.A. DeWoody. 2015. The impacts of inbreeding, drift, and selection on genetic diversity in captive breeding populations. Molecular Ecology 24:98-110.

Wells, K., B.W. Brook, R.C. Lacy, G.J. Mutze, D.E. Peacock, R.G. Sinclair, N. Schwensow, P. Cassey, R.B. O'Hara, and D.A. Fordham. 2015. Timing and severity of immunizing diseases in rabbits is controlled by seasonal matching of host and pathogen dynamics. Journal of the Royal Society Interface 12:2014184 http://dx.doi.org/10.1098/rsif.2014.1184

Heinsohn, R., M. Webb, R. Lacy, A. Terauds, R. Alderman, and D. Stojanovic. 2015. A severe predator-induced population decline predicted for endangered, migratory swift parrots (*Lathamus discolor*). Biological Conservation 186:75-82.

Lacy, R.C., K.C. Balcomb III, L.J.N. Brent, D.P. Croft, C.W. Clark, and P.C. Paquet. 2015. Report on Population Viability Analysis model investigations of threats to the Southern Resident Killer Whale population from Trans Mountain Expansion Project. Attachment E, Ecojustice – Written Evidence of Raincoast Conservation Foundation (A70286), National Energy Board (Canada). 120 pp. Available at http://docs.neb-one.gc.ca/fetch.asp?language=E&ID=A4L9G2.

Zhao, X., Y. Ueda, S. Kajigaya, G. Alaks, M.J. Desierto, D.M. Townsley, B. Dumitriu, J. Chen, R.C. Lacy, and N.S. Young. 2015. Cloning and molecular characterization of telomerase reverse transcriptase (TERT) and telomere length analysis of *Peromyscus leucopus*. Gene 568:8-18.

Canessa, S., G. Guillera-Arroita, J. Lahoz-Monfort, D.M. Southwell, D.P. Armstrong, I. Chadès, R.C. Lacy, and S.J. Converse. 2015. When do we need more data? A primer on calculating the value of information for applied ecologists. Methods in Ecology & Evolution 6:1219-1228.

Prowse, T.A.A., C.J.A. Bradshaw, S. Delean, P. Cassey, R.C. Lacy, K. Wells, M.

Aiello-Lammens, H.R. Akçakaya, and B.W. Brook. 2016. An efficient protocol for the sensitivity analysis of complex ecological models. Ecosphere 7(3):e01238. 10.1002/ecs2.1238

Jiménez-Mena, B., K. Schad, N. Hanna, and R.C. Lacy. 2016. Pedigree analysis for the genetic management of group-living species. Ecology and Evolution 6:3067-3078.

Miller, P.S., R.C. Lacy, R. Medina-Miranda, R. López-Ortiz, and H. Díaz-Soltero. 2016. Confronting the invasive species crisis with meta-model analysis: An explicit, two-species demographic assessment of an endangered bird and its brood parasite in Puerto Rico. Biological Conservation 196:124-132.

Manlik, O., J.A. McDonald, J. Mann, H.C. Raudino, L. Bejder, M. Krützen, R.C. Connor, M.R. Heithaus, R.C. Lacy, and W.B. Sherwin. 2016. The relative importance of reproduction and survival for the conservation of two dolphin populations. Ecology & Evolution 6:3496-3512. http://onlinelibrary.wiley.com/doi/10.1002/ece3.2130/full

Wells, K., P. Cassey, R.G. Sinclair, G.J. Mutze, D.E. Peacock, R.C. Lacy, B.D. Cooke, R,B. O'Hara, B.W. Brook, and D.A. Fordham. 2016. Targeting season and age for optimizing control of invasive rabbits. Journal of Wildlife Management 80:990-999. doi: 10.1002/jwmg.21093.

Willis, K., and R.C. Lacy. 2016. Use of animals with partially known ancestries in scientifically managed breeding programs. Zoo Biology 35:319-325.

Canessa, S., G. Guillera-Arroita, J. Lahoz-Monfort, D.M. Southwell, D.P. Armstrong, I. Chades, R.C. Lacy, and S. Converse. 2016. Adaptive management for improving species conservation across the captive-wild spectrum. Biological Conservation 199:123-131.

Fant, J.B., K. Havens, A.T. Kramer, S.K. Walsh, T. Callicrate, R.C. Lacy, M. Maunder, A. Hird Meyer, P.P. Smith. 2016. What to do when we can't bank on seeds: What botanic gardens can learn from the zoo community about conserving plants in living collections. American Journal of Botany 103:1541-1543.

Lacy, R.C., K.M. Kovacs, C. Lydersen, and J. Aars. 2016. Case Study 4. Exploring impacts of declining sea ice on polar bears and their ringed seal and bearded seal prey in the northern Barents Sea. Pages 77-81 in W.B. Foden and B.E. Young (eds.), IUCN SSC Guidelines for Assessing Species' Vulnerability to Climate Change. Version 1.0. Cambridge, UK and Gland, Switzerland: IUCN Species Survival Commission.

Pacioni, C., M.R. Williams, R.C. Lacy, P.B.S. Spencer, A.F. Wayne. 2017. Predators and genetic fitness: key threatening factors for the conservation of a bettong species. Pacific Conservation Biology 23:200-2122. http://dx.doi.org/10.1071/PC17002.

Williams, R., Lacy, R.C., Ashe, E., Hall, A., Lehoux, C., Lesage, V., McQuinn, I., Plourde, S. 2017. Predicting responses of St. Lawrence beluga to environmental change and anthropogenic threats to orient effective management actions. DFO Can. Sci. Advis. Sec. Res. Doc. 2017/027. v + 44 p.

Willoughby, J.R., J.A. Ivy, R.C. Lacy, J. Doyle, and J.A. DeWoody. 2017. Inbreeding and selection shape genomic diversity in captive populations: implications for the conservation of endangered species. PLOS ONE 12(4): e0175996. doi:10.1371/journal.pone.0175996.

Raboy, B.E., R.C. Lacy, T. Callicrate, & C.M. Lees. 2017. *METAMODEL MANAGER. User's*

Manual. Chicago Zoological Society, Brookfield, Illinois, USA. Available at: http://www.vortex10.org/MeMoMa.aspx.

Frankham, R., J.D. Ballou, K. Ralls, M.D.B. Eldridge, M.R. Dudash, C.B. Fenster, R.C. Lacy, and P. Sunnucks. 2017. Genetic Management of Fragmented Animal and Plant Populations. Oxford University Press, Oxford UK.

Malo, A.F., F. Martinez-Pastor, F. Garcia-Gonzalez, J. Garde, J.D. Ballou, and R.C. Lacy. 2017. A father effect explains sex-ratio bias. Proceedings of the Royal Society B 20171159. http://dx.doi.org/10.1098/rspb.2017.1159.

Ralls, K., J.D. Ballou, M.R. Dudash, M.D.B. Eldridge, C.B. Fenster, R.C. Lacy, P. Sunnucks, and R. Frankham. 2017. Call for a paradigm shift in the genetic management of fragmented populations. Conservation Letters doi: 10.1111/conl.12412.

Lacy, R.C., R. Williams, E. Ashe, K.C. Balcomb III, L.J.N. Brent, C.W. Clark, D.P. Croft, D.A. Giles, M. MacDuffee, and P.C. Paquet. 2017. Evaluating anthropogenic threats to endangered killer whales to inform effective recovery plans. Scientific Reports 7:14119. doi: 10.1038/s41598-017-14471-0.

Manlik, O., R.C. Lacy, and W.B. Sherwin. 2018. Applicability and limitations of sensitivity analysis for wildlife management. Journal of Applied Ecology 55:1430-1440. https://doi.org/10.1111/1365-2664.13044

Lacy, R.C., Malo, A.F., & Alaks, G. 2018. Maintenance of genetic variation in quantitative traits of a woodland rodent during generations of captive breeding. Conservation Genetics 19:789-802. doi: 10.1007/s10592-018-1054-y.

Pacioni, C., S. Sullivan, C.M. Lees, P.S. Miller, R.C. Lacy. 2018. *OUTBREAK User's Manual*. Chicago Zoological Society, Brookfield, Illinois, USA.

Lacy, R.C. Lessons from 30 years of Population Viability Analysis of wildlife populations. Zoo Biology (in press)

Johnson, K., A. Baker, K. Buley, L. Carrillo, R. Gibson, G. Gillespie, B. Johnson, R.C. Lacy, and K. Zippel. A process for assessing and prioritizing species conservation needs – going beyond the Red List. Oryx (in press)

Fenster, C.B., J.D. Ballou, M.R. Dudash, M.D.B. Eldridge, R. Frankham, R.C. Lacy, K. Ralls, & P. Sunnucks. Conservation and genetics. Yale Journal of Biology and Medicine (submitted)

Ballou, J.D., R.C. Lacy, K. Traylor-Holzer, K. Bauman, J.A. Ivy, P. Siminski, and C. Asa. Strategies for establishing and using genome resource banks in endangered species conservation. (submitted)

Lacy, R.C., K.M. Kovacs, C. Lydersen, and J. Aars. Linking PVA models to explore the impacts of declining polar ice on interconnected species in the arctic ecosystem. (submitted)

Ashe, E., R. Williams, F. Cipriano, C.W. Clark, C. Erbe, A. Hall, P. Hammond, R.C. Lacy, R. Reeves, B. Taylor, and N. Vollmer. Avoiding the data-gap trap: predicting sensitivity of abundant species to anthropogenic threats before declines can be detected. (submitted)

Software developed and distributed for professional use

PMx: Software for demographic and genetic analysis and management of populations. (Developed jointly with J. Ballou and J.P. Pollak). Used to guide management of captive populations of more than 1000 species globally.

Vortex: Simulation of interacting genetic, demographic, and environmental causes of extinction in small, isolated populations interconnected by occasional migration. Used by conservation and wildlife biologists to assist in the analysis and management of wild populations of 100s of species in more than 70 countries.

Vortex Adaptive Manager. Software for guiding adaptive management of wildlife populations.

Outbreak: Epidemiological simulation for modeling infectious disease. (Developed with J.P. Pollak, P.S. Miller, et al.)

MetaModel Manager: Flexible modeling platform for linking simulation models representing diverse processes (such as species interactions, habitat change, climate change, disease, and social systems) to provide more holistic risk assessments for wildlife populations. (Developed with J.P. Pollak.)

MMMacro: A dll library providing a macro script interpreter for use within system models. (MMMacroEntry provides a stand-alone program for writing and testing macro scripts.)

- Curriculum Vitae -
Short Form
PAUL C. PAQUET, Ph.D.

Address: P.O. Box 150, Meacham, SK Canada
Telephone No.: (306) 376 2015
Email: ppaquet@baudoux.ca
Date of Birth: 06 December 1948
Citizenship: Canadian, U.S.A.

Education

1966 - 1970 B.A., Philosophy, University of Santa Clara, Santa Clara, California.
1967 - 1968 Undergraduate, Zoology, University of California, Berkeley, California.
1970 - 1970 Graduate Philosophy, Oxford University, Oxford, England.
1970 - 1971 Post Bacc., Biology, Portland State University, Portland, Oregon.
1971 - 1972 Graduate Studies, Wildlife Management, Oregon State University, Corvallis, Oregon.
1972 - 1974 B.S., Zoology (Wildlife Biology), Arizona State University, Tempe, Arizona. Thesis topic: Distribution and movements of coyotes along the lower Colorado River, Arizona.
1976 - 1981 M.S., Biology (Ethology), Portland State University, Portland, Oregon. Thesis topic: Temporal and phenomenological aspects of social behavior in captive wolves.
1982 - 1988 Ph.D., Zoology, University of Alberta, Edmonton, Alberta. Dissertation topic: Behavioural ecology of sympatric wolves and coyotes in Riding Mountain National Park, Manitoba.
1989-1990 Postdoc, Yale University, New Haven, CT

Academic Appointments

1988/89 Assistant Professor, Department of Biology, Brandon University, Brandon, Manitoba
1989-2012 Adjunct Professor, Department of Biology, Brandon University, Brandon, Manitoba
1995-2006 Faculty Associate, Faculty of Graduate Studies, Guelph University, Guelph, Ontario
1994-2012 Adjunct Associate Professor, Faculty of Environmental Design, University of Calgary, Calgary, Alberta
1997-2001 Adjunct Professor, Department of Biology, University of Calgary, Calgary, Alberta
1997-2001 Adjunct Professor, Department of Zoology, University of Alberta, Edmonton, Alberta
2003-2012 Adjunct Professor, Dept. of Environment and Geography, University of

	Manitoba, Winnipeg
2003-	Honorary Research Associate, Department of Biology, University of New Brunswick, Fredericton
2006-2009	Adjunct Professor, Department of Veterinary Pathology, Western College of Veterinary Medicine, University of Saskatchewan
2012-	Adjunct Professor, Department of Geography, University of Victoria, Victoria, BC

Other Appointments

2000-2008	Senior Scientist, Conservation Biology Institute, U.S.A.
1995-2009	Research Fellow, World Wildlife Fund – Canada
2000-present	Senior Scientist, Raincoast Conservation Society, Canada
2005-present	Research Fellow, Rewilding Institute, U.S.A.
2005-2016	Society for Conservation Biology – International Policy Committee
2007-2009	Wildlife Society Canada – Policy Committee
2000-2014	International Union for Conservation of Nature Breeding Specialist Group
2015	International Union for Conservation of Nature Wolf Specialist Group
2017	International Union for Conservation of Nature WCPA Connectivity Conservation Specialist Group

Certification

1972 1977	Instructor, Outward Bound Schools; Kayaking, Snow, Ice and Rock Climbing, Mountaineering
1982	"Animal damage control in coastal forests of the Pacific Northwest." Cooperative Extension, U.S. Fish & Wildlife Service, Department of Interior.
1984	"Biotelemetry, methods and applications." Telonics Inc., Mesa, Arizona in conjunction with Lethbridge Community College, Lethbridge, Alberta.
1987	Instructor's Certification "Safety in bear country", Departments of Natural Resources, N.W.T. and Manitoba.
1988	"Wildlife Immobilization", Canadian Parks Service, Environment Canada

Professional Societies

1974-2014	The Wildlife Society, Washington D.C.
1974-2014	The American Society of Mammalogists, Kansas City, Missouri
1984-1989	The Wildlife Society of Canada
1984-2014	Canadian Field Naturalists
1985-1999	Canadian Society of Zoologists
1989-present	Society for Conservation Biology
1992-2004	New York Academy of Science
1994-present	American Association for the Advancement of Science
2003-present	American Institute of Biological Sciences

Committees and Boards

1986-1991	Riding Mountain Biosphere Reserve, Chairman, Manitoba
1989-2009	Central Canadian Rockies Wolf Project, Board of Directors, Canmore, AB
1991-1999	Board of Scientific Advisors, Canid Research Facility, Dalhousie University, Nova Scotia
1992-2008	Coordinator for World Wildlife Fund (Canada) Carnivore Conservation Program
1992-	Board of Directors, German Wolf Society, Cologne, Germany
1993-1999	Banff National Park Elk Advisory Committee, Banff National Park, Alberta
1993-1999	Scientific Advisor, European Wolf Federation, Liege, Belgium
1993-1999	Director of Gray Wolf Research, Tatra Mountains National Park Wolf Ecology Project, Tatra, Slovakia
1993-1999	Director of Gray Wolf Research, Slovakian Wolf Ecology Project, Slovakia
1994-1998	Advisory Board of the Environmental Research Center, University of Calgary, Calgary, AB.
1993-2001	Predator/Prey Study Steering Committee and Director of Research, Pukaskwa National Park, Pukaskwa, Ontario
1993-2005	East Slopes Steering Committee for Grizzly Bear Research in Central Canadian Rocky Mountains
1995-2000	Grizzly Bear Scientific Advisory Committee to Minister of Environment, British Columbia Provincial Grizzly Bear Strategy
1995-2000	Scientific Steering Committee, World Wild Fund for Nature - International, Pan-European Carnivore Conservation Strategy
1994-1999	Town of Canmore Wildlife Corridor Committee, Canmore Alberta.
1996	Columbia Basin Science Review Panel, U.S. Forest Service

1995	Tongas National Forest, Alaska - Scientific Review Committee. U.S. Forest Service
1997-2008	Northwest Territories, Ecology of Wolves in the Central Arctic, N.W.T., Research Associate, Yellowknife, Northwest Territories.
1997	Nez Pearce Wolf Recovery Scientific Advisory Committee, Idaho
1997-2003	Board or Directors and Founding Member, Conservation Biology Institute, Corvallis, Oregon.
1997	U.S. Forest Service Lynx Research Advisory Committee, Missoula, Mt.
1995-1997	Riding Mountain National Park Management Plan Science Advisory Committee, Riding Mountain National Park, Manitoba.
1998-2006	Animal Care Committee, American Society of Mammalogists
1999-2005	U.S. Fish & Wildlife Service, Red Wolf Reintroduction Advisory Committee
1996-2014	Parks and Wilderness Specialist Group; International Union for Conservation of Nature
2000-2014	Conservation Breeding Specialist Group, International Union for Conservation of Nature Species Specialists, Member and Strategic Associate
2002-2009	Board of Directors, Defenders of Wildlife Canada
2003-2007	Board of Directors, Wildlands League, USA
2004-2008	Chair, Science Advisory Committee, Infectious Wildlife Disease National Strategy, Canada
2004-present	Chair, National Science Advisory Committee, for Wildlife Tuberculosis, Riding Mountain, Manitoba
2008-2015	Board of Directors, Society for Conservation biology
2012-present	Woodland Caribou Technical Committee, Province of Saskatchewan
2014	Canid Specialist Group, International Union for Conservation of Nature Species Specialists, Member and Strategic Associate
2017-03-21	Connectivity Conservation Specialist Group, International Union for Conservation of Nature, Member

Periodicals and Reports

Paquet, P.C. 1974. Small mammals of the Colorado River islands (Arizona). Arizona Fish and Game Bull. 56.

Paquet, P.C. 1974. Coyote literature review. Special report, Arizona State University Press, Tempe, Ariz.

Paquet, P.C. 1976. Wolves. Portland Zoological Society Magazine, Portland Zoological Gardens, Portland, Oregon.

Paquet, P.C., and J.O. Sullivan. 1977. Behavior of wild canids: Social systems of wolves in large and small enclosures. Proc. Amer. Assoc. Zool. Parks & Aquar., Hills Co., Topeka, Kansas.

Paquet, P.C., and J.O. Sullivan. 1978. Management of wolves in captivity. Proc. W. Psychol. Assoc., San Francisco State Univ., San Francisco, California.

Paquet, P.C. 1981. Behavior of Domesticated Dogs. Pamphlet, Multnomah County Animal Control, Multnomah County, Oregon, 12 pp.

Carbyn, L.N., D.M. Meleshko, and P.C. Paquet. 1983. Ecological studies of wolves and coyotes in Riding Mountain National Park, Manitoba. Canadian Wildlife Service Annual Report: 15 June 1982 to 31 March 1983. 60 pp.

Meleshko, D.M., and P.C. Paquet. 1983. Annual classified ungulate survey, Riding Mountain National Park, Manitoba. Canadian Wildlife Service Report, Large Mammal System Study Series.

Paquet, P.C., and D.M. Meleshko. 1984. Annual classified ungulate survey, Riding Mountain National Park, Manitoba. Canadian Wildlife Service Report.

Paquet, P.C., D.M. Meleshko, and L.N. Carbyn. 1985. Annual classified ungulate survey, Riding Mountain National Park, Manitoba. Canadian Wildlife Service Report.

Carbyn, L.N., Paquet, P.C., and D.M. Meleshko. 1985. Ecological studies of wolves and coyotes in Riding Mountain National Park, Manitoba. Canadian Wildlife Service Annual Report: 1 April 1983 to 31 December 1984.

Pesendorfer, J., P. C. Paquet, and L. N. Carbyn. 1986. A comparison of the 1984 and 1985 nocturnal howling surveys, RMNP, Manitoba. LMSS Series, Rep. No. 18.Carbyn, L. N., D. Meleshko, P. C. Paquet, S. Mckinlay, D. Burles, and J. Pessendorfer. 1986. Ecological studies of wolves and coyotes in Riding Mountain National Park, Manitoba. Canadian Wildlife Service Progress Report 3.

Carbyn, L.N., and P.C. Paquet. 1986. Long distance movement of a coyote from Riding Mountain National Park. Journal of Wildlife Management 50:89.

Meleshko, D.M., and P.C. Paquet. 1986. Annual classified ungulate survey, Riding Mountain National Park, Manitoba. Canadian Wildlife Service Report.

Paquet, P.C. 1986. Wolves revisited. Nature Canada 15:54.

Paquet, P.C., and L.N. Carbyn. 1986. Wolves, Canis lupus, killing denning black bears, Ursus americanus, in the Riding Mountain National Park area. Canadian Field-Naturalist 100:371-372.

Pesendorfer J., P.C. Paquet, and L.N. Carbyn. 1986. A comparison of the 1984 and 1985 nocturnal howling surveys, Riding Mountain National Park, Manitoba. Canadian Wildlife Service Report No. 18, Large Mammal System Study Series, 18 pp.

Carbyn, L.N., P.C. Paquet, and D.M. Meleshko. 1987. The Wolves of Riding Mountain. Canadian Wildlife Service Report, Large Mammal System Study Series.

Paquet, P.C. 1987. Canid howling survey. Riding Mountain National Park, Manitoba. Canadian Wildlife Service Report, Large Mammal System Study Series.

Paquet, P.C., Crichton, V.F.J., and Wotten. D.L. 1988. A study of cadmium levels in Manitoba wildlife. 1987 Progress Report. Prepared for Environment Canada and World Wildlife Fund Canada, Toxicology Fund.

Kiliaan, H.P.L., Mamo, C. and Paquet, P.C., 1991. A coyote, *Canis latrans*, and badger, *Taxidea taxus*, interaction near Cypress Hills Provincial-Park, Alberta. Canadian Field-Naturalist, *105*:122-123.

Gibeau, M, and Paquet, P.C. 1991. Evaluation of telezol for immobilization of black bears. Wildlife Society Bulletin 19:400-402.

Paquet, P.C. 1991. Winter spatial relationships of wolves and coyotes in Riding Mountain National Park, Manitoba. Journal of Mammalogy 72:397-401.

Paquet P.C. 1991. Black bear ecology in the Riding Mountains. Final report. Prepared for Manitoba Natural Resources and Canadian Park Service by John/Paul & Associates. 143 pp.

Paquet, P.C. 1991. Scent marking behavior of sympatric wolves (*Canis lupus*) and coyotes (*C. latrans*) in Riding Mountain National Park. Canadian Journal of Zoology 69:1721-1727.

Irwin, G.H., Purves, H., Paquet, P.C., and J.G. Woods. 1992. An intervener submission to the Natural Resource Board of Alberta on behalf of Environment Canada relating to application #9103 by Three Sisters Golf Resorts Inc. Recreational and Tourist Development in the Bow-Canmore Corridor. Environment Canada, Banff, AB. 72pp.

McCallum, M.J. and P.C. Paquet. 1992. Preliminary wildlife study and analysis of ungulate travel corridors on CADCO property, Canmore, Alberta. Prepared for Canmore Alpine Development Company Ltd. 72pp.

Paquet, P.C. 1992. Prey use strategies of sympatric wolves and coyotes in Riding Mountain National Park, Manitoba. Journal of Mammalogy 73:337-343.

Purves, H.D., White, C.A., and P.C. Paquet. 1992. Wolf and grizzly bear habitat use and displacement by human use in Banff, Yoho, and Kootenay National Parks: a preliminary analysis. Canadian Parks Service, Banff. AB. 54pp.

McCallum, M.J. and P.C. Paquet. 1993. Stone Creek Properties Inc. wildlife management plan, Canmore, Alberta. Prepared for Stone Creek Properties by McCallum Paquet Associates. 95pp.

McTavish, C. and Paquet, P.C. 1993. Behavioral ecology of gray wolves in Kootenay National Park, British Columbia. Annual Report. Prepared for Parks Canada.

Gibeau, M.L., Paquet, P.C., Herrero, S., J. Jorgenson, and G. Green. 1994. Wildlife corridors in the Bow Valley, Alberta: an analysis. Prepared for the Inter-government Committee on Wildlife Corridors. Canmore, AB. 37pp.

Keister, R.A., Eckhardt, C., Benkman, C.W., Hansen, AJ., Houck, O. Jarvis, R.L., Lande, R., Lidicker, W.Z., McCullough, D.R., McLellan, B., Marcot, B., Mariani, J., Paquet, P.C., Pletscher, D., Powell, R., Ratti, J., Scott, J.M., Schaffer, M.L., Smith, C.C., Taber, R.D., Walters, J. 1994. Wildlife management and conservation biology on the Tongass National Forest: A synthentic review with recommendations. Pacific Northwest Research Station. USDA Forest Service, Corvallis, Ore.

Krizan, P., Neale, G., Paquet, P.C. 1994. Behavioral ecology of gray wolves in Pukaskwa National Park, Ontario, Annual Report. Prepared for Parks Canada.

Pacas, C., and Paquet, P.C. 1995. Analysis of black bear home range using a geographic information system. International Conference on Bear Research and Management. 9:419-425.

McCallum, M.J. and P.C. Paquet. 1995. Special features in Yoho National Park, MT. Prepared for Parks Canada. Yoho National Park, B.C.

McCallum, M.J. and P.C. Paquet. 1995. 1994 Wildlife Monitoring on the SilverTip property, Canmore, AB. Prepared for Stone Creek Properties by McCallum Paquet Associates, Canmore, Alberta. 47pp.

Paquet, P.C., and Hackman, A. 1995. A large carnivore conservation strategy for the Rocky Mountains. World Wildlife Fund (Canada) and World Wildlife Fund (USA). 52pp.

Alexander, S., C. Callaghan, P.C. Paquet and N. Waters. 1996. GIS predictive models for habitat use by wolves (*Canis lupus*). Conference Proceedings: CD-ROM. GIS '96: Ten Years of Excellence. Vancouver, BC. March 17-20, 1996.

Clark, T.W., Paquet, P.C., and Purlee, P. (eds) 1996. Large Carnivore Conservation in the Rocky Mountains of the United States and Canada. Special Section. Conservation Biology 10:936-1055.

Clark, T.W., Paquet, P.C., and Curlee, P.A. 1996. Introduction: Special Section: Large Carnivore Conservation in the Rocky Mountains of the United States and Canada. Conservation Biology 10:936-939.

Clark, T.W., Paquet, P.C., and Curlee, P.A. 1996. General lessons and positive trends in large carnivore Conservation: Special Section: Large Carnivore Conservation in the Rocky Mountains of the United States and Canada. Conservation Biology 10:1055-1058.

P.C. Paquet and C. Apps. 1996. Section 3.5.3 on gray wolves. In Herrero, S. and Herrero, J. Cheviot Mine Project: Specific and cumulative environmental effects analysis for mammalian carnivores. Prepared for Cardinal River Coal Ltd. Hinton, AB. 122pp

McCallum, M.J. and P.C. Paquet. 1996. 1995 Wildlife Monitoring on the SilverTip property, Canmore, AB. Prepared for Stone Creek Properties by McCallum Paquet Associates, Canmore, Alberta. 47pp.

Noss, F. R., Quigley, H.B., Hornocker, T.M., and Paquet, P.C. 1996. Conservation biology and carnivore conservation in the Rocky Mountains. Conservation Biology 10:949-963.

P5 Study. 1996. Interim report on ecology of gray wolves and associated prey species in the Greater Pukaskwa Ecosystem, Ontario, 1994-1996. Prepared by F. Burrows, P. Krizan, G. Neale, and P. Paquet for Pukaskwa National Park, ON.

Weaver, J.L., Paquet, P.C., and L.F. Ruggierio. 1996. Resilience and Conservation of Large Carnivores in the Rocky Mountains. Conservation Biology 10:964-976.

Alexander, S., P.C. Paquet and N. Waters. 1997. Playing God with GIS: Uncertainty in

Wolf Habitat Suitability Models. Conference Proceedings: GIS World '97. Vancouver, BC. February 17-20, 1997.

Sawyer, M.D., D. Mayhood, P. Paquet, C. Wallis, R. Thomas, and W. Haskins. 1997. Southern East Slopes Cumulative Effects Assessment Project. Prepared for Morrison Petroleum Ltd. Calgary, AB. 291 pp.

Donelon, S. & P.C. Paquet. 1997. Technical report on development of a decision support model for the Lake O'hara socio-ecologic study. A Background report for the GIS decision-support model for the Lake O'Hara/McArthur Valley Socio-ecological Study. Parks Canada.

McRory, W. McTavish, C. and P.C. Paquet. 1998. Grizzly bear background research document1993-1996 for GIS bear encounter risk model, Yoho National Park, B.C. A Background report for the GIS decision-support model for the Lake O'Hara/McArthur Valley Socio-ecological Study. Parks Canada.

Crichton, V. and P.C. Paquet. 1999. Cadmium in Manitoba's Wildlife. Alces 36:205-216.

Paquet, P.C., Noss, R.F., Carroll, C., and S. Alexander. 1999. Conservation biology primer and carnivores as conservation species. Prepared for Sierra Club of British Columbia and Central Coast LRMP.

Wilson, P. J., S. Grewal, I. D. Lawford, J. N. M. Heal, A. G. Granacki, D. Pennock, J. B. Theberge, M. T. Theberge, D. R. Voigt, W. Waddell, R. E. Chambers, P. C. Paquet, G. Goulet, D. Cluff, and B. N. White. 2000. DNA profiles of the eastern Canadian wolf and the red wolf provide evidence for a common evolutionary history independent of the gray wolf. Canadian Journal of Zoology 78:1-11.

Carroll, C., Noss, R.F., and P.C. Paquet. 1999. Carnivores as focal species for conservation planning in the Rocky Mountain region. World Wildlife Fund Canada. Toronto, Ontario, Canada. 61pp.

Carroll, C., Paquet, P.C., & R.F. Noss. 1999. Modeling carnivore habitat in the Rocky Mountain region. A literature review and suggested strategy. World Wildlife Fund Canada. Toronto, Ontario, Canada. 104pp.

Terborgh, J., J. Estes, P. C. Paquet, K. Ralls, D. Boyd-Heger, B. Miller, and R. Noss. 1999. The role of top carnivores in regulating terrestrial ecosystems. Wild Earth 9:42-56.

Darimont, C.T. and P.C. Paquet. 2000. The gray wolves (Canis lupus) of British

Columbia's coastal rainforests: Findings from year 2000 pilot study and conservation assessment. Prepared for Raincoast Conservation Society. Victoria, BC. 62pp.

Carroll, C., Noss, R.F., and P.C. Paquet. 2001. Carnivores as focal species for conservation planning in the Rocky Mountain Region. Ecological Applications 11:961-980.

Walton, H,. D. Cluff, P. C. Paquet, and M.A. Ramsay. 2001. Performance of two models of satellite collars for wolves. Wildlife Society Bulletin 29:180-186.

Walton, H,. D. Cluff, P. C. Paquet, and M.A. Ramsay. 2001. Movement patterns of barren-ground wolves in the Central Canadian arctic. Journal of Mammalogy 82:867-876.

Paquet, P.C., Vucetich, J.A. Phillips, M.K. and L.M. Vucetich et al. 2001. Mexican wolf recovery: three-year program review and assessment. Prepared by the Conservation Breeding Specialist Group (CBSG), Apple Valley, Minnesota; prepared for the United States Fish and Wildlife Service, Albuquerque, New Mexico. 86pp.

Fascione, N., Osborn, L.G.L., Kendrot, S.R., and P.C. Paquet. 2001. Canis soupus: Eastern wolf genetics and its implications for wolf recovery in the Northeast United States. Endangered Species Update 18:159-163.

Paquet, P.C., Burrows, F., Forshner, A., Neale, G., and K. Wade. 2002. Blastomycosis in a free ranging wolves, Canis lupus, on the North Shore of Lake Superior, Ontario - a response to P. Krizan. Canadian Field Naturalist 115:185.

Paquet, P.C. and Darimont, C.T. 2002. Yeo Island Wolf Home Site Recommendation A Proposed Solution To The Potential Conflict Between The Home Site Requirements Of Wolves And Areas Targeted For Timber Harvest Prepared For The Heiltsuk Nation, Western Forest Products, Raincoast Conservation Society.

Alexander, S.M., Duke, D.L., and P.C. Paquet. 2002. Modeling carnivore habitat-use, travel patterns and human activity around the town of Canmore. Prepared for the Wilburforce Foundation, Seattle, WA.

Carroll, C., Noss, R.F., and Paquet, P.C. 2002. Rocky Mountain carnivore project final report. Prepared For World Wildlife Fund Canada, Toronto, ON.

Hebblewhite, M., D.H. Pletscher, and P.C. Paquet. 2002. Elk population dynamics in areas with and without predation by recolonizing wolves in Banff National Park, Alberta. Canadian Journal of Zoology 80:789-799.

Darimont, C.T. and P.C. Paquet. 2002. The Gray Wolves, Canis lupus, of British Columbia's Central and North Coast: distribution and conservation assessment. Canadian Field-Naturalist 116:416-422.

McCrory, W., Paquet, P., and Cross, B. 2003. Assessing conservation values for the gray wolf and sitka deer of the B.C. Central Coast Rainforest.

Cluff, D., M. Musiani, P.F. Frame, P. Paquet, and C.C. Gates. 2003. Multiple litters at den sites, Northwest Territories Wolf Notes 7**:**1-8.

Darimont, C., Gerwing, K, Paquet, P., Reid, B., McCrory, W. and Cross, B. 2003. Preliminary modeling of deer winter range in Heiltsuk Territory on the Central Coast of British Columbia. (Summary reference document to accompany maps) Prepared for the Heiltsuk Nation and Raincoast Conservation Society, British Columbia.

Darimont, C.T., T.E. Reimchen and P.C. Paquet. 2003. Foraging behaviour by gray wolves on salmon streams in coastal British Columbia. Canadian Journal of Zoology 81:349-353.

Hebblewhite, M.D., Paquet, P.C., and D.H. Pletscher. 2003. Development and application of a ratio-estimator to estimate wolf killing rates and variance in a multiple prey system. Wildlife Society Bulletin 31:933–946

Hebblewhite, M.D., D.H. Pletscher, and Paquet, P.C. 2003. Elk population dynamics after wolf recolonization in the Bow Valley of Banff National Park. Research Links 11:1-13

Carroll, C., Noss, R.F., Paquet, P.C., and Schumaker, N.H. 2003. Integrating population viability analysis and reserve selection algorithms into regional conservation plans. Ecological Applications 13: 1773–1789.

Musiani, M. and P.C. Paquet. 2004. Wolf Persecution, Protection, and Restoration in Canada and the United States. Bioscience, 54:50-60.

Gilbert, B., Craighead, L., Horejsi, B., Paquet, P., and W. McCrory. 2004. Scientific criteria for evaluation and establishment of grizzly bear management areas in British Columbia. Panel of Independent Scientists, Victoria, B.C. 16pp.

Paquet, P.C., C.T. Darimont, R. J. Nelson, and K. Bennett. 2004. A critical assessment of protection for key wildlife and salmon habitats under the proposed British Columbia Central Coast Land and Resource Management Plan. Raincoast Conservation Society. 23pp.

Carroll, C., Noss, R.F., Paquet, P.C., and Schumaker, N.H. 2004. Extinction debt of protected areas in developing landscapes. Conservation Biology 18: 1110-1120.

McLoughlin, P.D., Walton, L., Cluff, H.D., Paquet, P. 2004. Hierarchical habitat selection by tundra wolves. Journal of Mammalogy 85:576-580.

Frame, P.F., D.S. Hik, H.D. Cluff, and P.C. Paquet. 2004. Long foraging movement of a denning tundra wolf. Arctic 58: 196-203.

Forshner, S. A., P. Paquet, F. G. M. Burrows, G. K. Neale, and K. D. Wade. 2004. Demographic patterns and limitations of wolves (*Canis lupus*) in and near Pukaskwa National Park, Ontario, Canada. Canadian Field Naturalist 118:95-104.

Carroll, C., Noss, R.F., and P.C. Paquet. 2004. A proposed wildlands network for carnivore conservation in the Rocky Mountains. Wild Earth, Spring: 38-41

Darimont, C. T., M. H. H. Price, N. N. Winchester, J. Gordon-Walker and P. C. Paquet. 2004. Predators in natural fragments: foraging ecology of wolves in British Columbia's central and north coast archipelago. Journal of Biogeography 31: 1867–1877

Paquet, P. C., C. T. Darimont, C. Genovali, and F. Moola. 2004-2005. In the Great Bear Rainforest: island-hopping gray wolves give new insights into island biogeography. Wild Earth Fall/Winter: 20-25

Paquet, P., C. Darimont, C. Genovali, and F. Moola. 2005. Last of the best. Wolf Print. The UK Wolf Conservation Trust. Issue 24: 7-9.

Paquet, P. C. and S. M. Alexander. 2004-2005. Banff National Park: how helpful is highway mitigation? Wild Earth Fall/Winter: 70-71.

Paquet, P. C. and R. K. Brook. 2005. Island use as an anti-predator tactic by parturient elk and nursery herds in Riding Mountain National Park, Manitoba. Wildlife Society Bulletin.

Darimont, C. T., P. C. Paquet, T. E. Reimchen, and V. Crichton. 2005. Range expansion by moose into coastal temperate rainforests of British Columbia, Canada. Diversity and Distributions 11: 235–239

Jickling, R., and P.C. Paquet. 2005. Wolf stories: Reflections on science, ethics, and epistemology. Environmental Ethics 27:115-134.

Alexander, S. M., P. C. Paquet, T. B. Logan, and D. J. Saher. 2005. Snow-tracking versus radio-telemetry for predicting wolf-environment relationships in the Rocky Mountains of Canada. Wildlife Society Bulletin 33: 1216-1224.

Hebblewhite, M., C. White, C. Nietvelt, J. Mckenzie, T. Hurd, J. Fryxell, S. Bayley, and P. C. Paquet. 2005. Human activity mediates a trophic cascade caused by wolves. Ecology 86: 1320–1330

Price, M. H., C. T. Darimont, N. N. Winchester, and P. C. Paquet. 2005. Facts from faeces: Prey remains in Wolf, Canis lupus, faeces revise occurrence records for mammals of British Columbia's coastal archipelago. The Canadian Field Naturalist 119: 192-196.

Alexander, S. M., Waters, N. M. and Paquet, P. C. 2005. Traffic volume and highway permeability for a mammalian community in the Canadian Rocky Mountains. Canadian Geographer / Le Géographe Canadien 49: 321-331

Paquet, P.C., C.T. Darimont, F.M. Moola, and C. Genovali. 2005. Connectivity where the land meets the sea; preserving the last of the best. Wild Earth 14: 21-25

Paquet, P.C., C.T. Darimont, and C. Genovali. 2006. The Great Bear Rainforest; Home of island-hopping wolves. Howlings Magazine. Winter 2005/2006.

Paquet, P.C., and C.T. Darimont. 2006. Old Growth, New Concern. Monday Magazine. August 30, 2006.

Theberge, J. B., M. T. Theberge, J. A. Vucetich, and P. C. Paquet. 2006. Pitfalls of applying adaptive management to a wolf population in Algonquin Provincial Park, Ontario. Environmental Management 37: 451-460.

Alexander, S. M., T. B. Logan, P. C. Paquet. 2006. Spatio-temporal co-occurrence of cougar (*Felis concolor*), wolves (*Canis lupus*) and their prey during winter: A comparison of two analytical methods. Journal of Biogeography 33: 2001-2012.

Paquet, P. C. and E. G. Walker. 2006. Review of investigative findings relating to the death of Kenton Carnegie At Points North, Saskatchewan. Prepared for and submitted to Office of the Chief Coroner Saskatchewan Justice #920, 1801 Hamilton Street Regina, Saskatchewan S4P 4B4. 32 pp.

Bryan, H., C.T. Darimont, T.E. Reimchen, and P.C. Paquet. 2006. Early ontogenetic diet in wolves, Canis lupus, of coastal British Columbia. Canadian Field-Naturalist 120:61-66.

Darimont, C. T., P. C. Paquet, and T. E. Reimchen. 2007. Stable isotopic niche predicts fitness in a wolf-deer system. Biological Journal of the Linnaean Society 90: 125-137.

Stronen, A. V, Brooks, R. K., Paquet, P. C., and S. Mclachlan. 2007. Farmer attitudes toward wolves: Implications for the role of predators in managing disease. Biological Conservation 135: 1-10.

Stronen, A., P.C. Paquet, S. Herrero, S. Sharpe, N. Waters. 2007. Translocation and Recovery Efforts for the Telkwa Caribou, Rangifer tarandus caribou, Herd in westcentral British Columbia, 1997 – 2005. Canadian Field-Naturalist. 121:155-163.

Nyhus, P. J., R. Lacy, F. R. Westley, P. Miller, H. Vredenburg, P. Paquet, and J. Pollak. 2007. Tackling biocomplexity with meta-models for species risk assessment. Ecology and Society 12(1): 31. [online] URL: http://www.ecologyandsociety.org/vol12/iss1/art31/

Musiani M., Leonard J. A., Cluff H. D., Gates C. C., Mariani S., Paquet P. C., Vilà C., Wayne R. K. 2007. Differentiation of tundra and boreal coniferous forest wolves: genetics, coat color and association with migratory caribou. Molecular Ecology 16: 4149-4170

Darimont, C.T., P.C. Paquet, and T.E. Reimchen. 2007. Stable isotopic niche predicts fitness of prey in a wolf-deer system. Biological Journal of the Linnean Society 90: 125-137

Apps, C. D., J. L. Weaver, P. C. Paquet, B. Bateman and B. N. McLellan. 2007. Carnivores in the southern Canadian Rockies: Core areas and connectivity across the Crowsnest Highway. Wildlife Conservation Society Canada Conservation Report No. 3. Toronto, Ontario, Canada.

Trapp, J.R., Beier, P., Mack, C., Parsons, D.R., and P.C. Paquet. 2008. Wolf, Canis lupus, den site selection in the Rocky Mountains. Canadian Field-Naturalist 122: 49-56.

Darimont, C. T., P. C. Paquet, and T. E. Reimchen. 2008. Spawning salmon disrupt tight trophic coupling between wolves and ungulate prey in coastal British Columbia. BMC Ecology 8: 14

Darimont, C.T., T.E. Reimchen, H. Bryan, and P.C. Paquet. 2008. Faecal-centric approaches to wildlife ecology and conservation; methods, data and ethics. Wildlife Biology in Practice 4: 73-87

Darimont, C. T., Paquet, P. C. and T. E. Reimchen. 2009. Landscape heterogeneity and marine subsidy generate extensive intrapopulation niche diversity in a large terrestrial vertebrate. Journal of Animal Ecology 78: 126–133

Muñoz-Fuentes, V., C.T. Darimont, R.K. Wayne, P.C. Paquet, and J.A. Leonard. 2009. The genetic legacy of extirpation and re-colonization in Vancouver Island wolves. Conservation Genetics. Early edition. www.pnas.org_cgi_doi_10.1073_pnas.09007871106

Muñoz-Fuentes, V., C.T. Darimont, R.K. Wayne, P.C. Paquet, and J.A. Leonard. 2009. Ecological factors drive genetic differentiation in British Columbia gray wolves. Journal of Biogeography 36: 1516-1531.

Kinnison, M.T., E.P. Palkovacs, C.T. Darimont, S.M. Carlson, P.C. Paquet, and C.C. Wilmers. 2009. Some cautionary notes on fisheries evolutionary impact assessments. Proceedings of the National Academy of Sciences. Early edition, www.pnas.org_cgi_doi_10.1073_pnas.09007871106

Darimont, C.T., S.M. Carlson, M.T. Kinnison, P.C. Paquet, T.E. Reimchen, and C.C. Wilmers. 2009. Reply to Koons: Harvest-related trait changes in an increasingly variable world. Proceedings of the National Academy of Sciences 106: E33.

Darimont, C.T., S.M. Carlson, M.T. Kinnison, P.C. Paquet, T.E. Reimchen, and C.C. Wilmers. 2009. Human predators outpace other agents of trait change. Proceedings of the National Academy of Sciences 106: 952-954 (Research Highlight and News & Views in Nature, F1000 Biology Recommended Paper; global media coverage in popular press, e.g. New York Times)

Darimont, C.T., P.C. Paquet, and T.E. Reimchen. 2009. Landscape heterogeneity and marine subsidy generate extensive niche variation in a terrestrial carnivore. Journal of Animal Ecology 79: 126-133

McCrory, W.P. and P. Paquet. 2009. Proposed bear-viewing strategy for the K’ztim-a-deen (Khutzeymateen) Grizzly Bear Sanctuary & K’tzim-a-deen Inlet Conservancies, British Columbia. Report for the K’tzim-a-deen Management Committee & Planning Process, Prince Rupert, B.C.

Mathews, F., D.T. Blumstein, C. Darimont, K. Chan, L. Dill, D. Fraser, J. Kirkwood, K. Littin, D. Lusseau, and P. Paquet. 2010. Uniting wild animal welfare and conservation: guiding principles. Animal Conservation.

Bryan, H.M., Sim, K.A., Darimont, C.T., Paquet, P.C., Wagner, B.W., Muñoz-Fuentes, V., Smits, J.E., and Chilton, N.B. 2010. Identification of *Parelaphostrongylus odocoilei* (Nematoda: Protostrongylidae) first-stage larvae in the feces of gray wolves (*Canis lupus*) by molecular methods. Journal of Wildlife Diseases 46: 297-302.

Paquet, P.C., and C.T. Darimont. 2010. Wildlife conservation and animal welfare: two sides of the same coin? Journal of Animal Welfare 19: 177-190.

Stronen, A.V., Forbes, G.J., Sallows, T., Goulet, G., Musiani, M., and P. C. Paquet. 2010. Wolf body mass, skull morphology and mitochondrial DNA haplotypes in the Riding Mountain National Park region of Manitoba, Canada. Canadian Journal of Zoology 88: 496-507

Fox, C.H., Paquet, P.C., Reimchen, T.C. 2010. Active American black bear dens adjacent to a marine beach used for foraging. Ursus 21:195–197.

Darimont, C.T., Bryan, H.M., Carlson, S.M., Hocking, M.D., MacDuffee, M., Paquet, P.C., Price, M. H.H., Reimchen, T.E., Reynolds, J.D., and Wilmers, C. 2010. Salmon for terrestrial protected areas. Conservation Letters 3:379-389.

Stronen, A.V., Sallows, T. Forbes, G.J., and P.C. Paquet. 2011. Disease and parasite burden in an increasingly isolated wolf population. Journal of Wildlife Diseases 47:222–227

Bryan, H.M., Darimont, C.T., Paquet, P.C., Ellis, J.A., Goji, N., Gouix, M. and Smits, J.E. 2011. Exposure to infectious agents in dogs in remote coastal British Columbia: possible sentinels of diseases in wildlife and people. Canadian Journal of Veterinary Research 75:11-17.

Stronen, A.V., Forbes, G.J., Paquet, P. C., Goulet, G., Sallows, T., and M. Musiani. 2011. Dispersal in a plain landscape: short-distance genetic differentiation in southwestern Manitoba wolves, Canada. Conservation Genetics 13:359-371 DOI 10.1007/s10592-011-0290-1

Stronen AV, Schumaker NH, Forbes GJ, Paquet PC, Brook RK. 2011. Landscape resistance to dispersal: predicting long-term effects of human disturbance on a small and isolated wolf population in southwestern Manitoba, Canada. Environmental Monitoring and Assessment. Published Online DOI 10.1007/s10661-011-2469-9

Nelson, M.P., Vecetich, J.A., Paquet, P.C. and J.K. Bump. 2011. An adequate construct? North American Model: What's flawed, what's missing, what's needed. The Wildlife Professional. Summer: 58-60

Daisuke Kawai, Caroline H. Fox, Paul C. Paquet and Falk Huettmann. Accepted. Predictive performances of 3 models for seabird sistribution and abundance estimates; Random Forests, Boosted Regression Trees, and Generalized Additive Model. Ecological Applications

Darimont, C.T., Artelle, K., Bryan, H.M., Genovali, C., MacDuffee, M., and Paquet, P.C. Grizzlies, Salmon, and People: Traveling the Upstream Journey to a Sustainable Future. Prepared for a Bear Anthology edited by Lisa M. Kemmerer, in press August 2011.

Vander Wal, E.; Paquet, P.; and J. Andrés. 2012. Influence of landscape and social interactions on transmission of communicable disease in a social cervid. Molecular Biology 21: 271–1282 doi: 10.1111/j.1365-294X.2011.05431.x

Nelson, B., Hebblewhite, M., Ezenwa, V., Shury, T., Merrill, E.H., Paquet, P.C., Schmiegelow, F., Seip, D., Skinner, G., Webb, N. 2012. Seroprevalence of canine parvovirus and distemper in wolves in the Canadian Rocky Mountains. Journal of Wildlife Diseases 48:68-76.

Service, C., T. Nelson, W. McInnes, P.C. Paquet & C.T. Darimont. 2012. Evaluating external risks to protected areas; the proposed Enbridge Northern Gateway pipeline in British Columbia, Canada. Natural Areas Journal. 32: 500-509. DOI: http://dx.doi.org/10.3375/043.032.0404URL: http://www.bioone.org/doi/full/10.3375/043.032.0404

Levi, T., C. T. Darimont, M.M. MacDuffee, M. Mangel, P.C. Paquet, & C.C. Wilmers. 2012. Using grizzly bears to assess economic and ecosystem tradeoffs in Pacific salmon management. PLoS Biology 10: e1001303.

Bryan, H.M. C.T. Darimont, J. Hill, P.C. Paquet, R.C.A. Thompson, B. Wagner, & J. E.G. Smits. 2012. Seasonal and biogeographic patterns of gastrointestinal parasites in large carnivores; wolves in a coastal archipelago. Parasitology 139: 781-790.

Stronen, A.V., Tessier, N., Jolicoeur, H., Paquet, P.C., Hénault, M., Villemure, M., Patterson, B.R., Sallows, T., Goulet, G. and F.J. Lapointe. 2012. Canid hybridization: contemporary evolution in human-modified landscapes. Ecology and Evolution 1-13.

Vander Wal, E., Paquet, P., and J. Andrés. 2012. Influence of landscape and social interactions on transmission of communicable disease in a social cervid. Molecular Biology 21: 271–1282 doi: 10.1111/j.1365-294X.2011.05431.x

van Beest, F.M., Vander Wal, E., Stronen, A.V., Paquet, P.C. and R.K. Brook. 2013. Temporal variation in site fidelity: Scale-dependent effects of forage abundance and predation risk in a non-migratory large herbivore. Oecologia. 173:409–420 DOI 10.1007/s00442-013-2647-2

Vander Wal, E., Edye, I., Paquet, P.C., Coltman, D.W., Bayne, E., R.K. Brook, R.K., and J.A. Andres. 2013. Juxtaposition between an unstructured white-tailed deer population and a structured elk population: implications for disease transmission in a sympatric cervid community. Evolutionary Applications. 6:1001-1111.

Vander Wal, E., Paquet, P.C., Messier, F., and P.D. McLoughlin. 2013. Effects of phenology and sex on social proximity in a gregarious ungulate Canadian Journal of Zoology. 91:601–609 dx.doi.org/10.1139/cjz-2012-0237

Stronen, A.V. and Paquet, P.C. 2013. Perspectives on the conservation of wild hybrids. Biological Conservation. 167:390–395. http://dx.doi.org/10.1016/j.biocon.2013.09.004

Artelle, K.A., S.C. Anderson, A.B. Cooper, P.C. Paquet, J.D. Reynolds, C.T. Darimont. 2013. Confronting uncertainty in wildlife management: performance of grizzly bear management. PLoS ONE 8(11): e78041. doi:10.1371/journal.pone.0078041

MacDuffee, M., A.R. Rosenberger, R. Dixon, M.H.H. Price, and P.C. Paquet. 2013. Embroiled, Volume 1: Salmon, tankers and the Enbridge Northern Gateway Proposal. Raincoast Conservation Foundation. Sidney, British Columbia. Vers 01-13, pp. 107.

Bryan, H.M., C.T. Darimont, P.C. Paquet, K.E. Wynne-Edwards and J.E. Smits. 2013. Stress and reproductive hormones in grizzly bears reflect nutritional benefits and social consequences of a salmon foraging niche. PLOS ONE

Vander Wal, E., P.C. Paquet, F. Messier, and P.D. McLoughlin. 2013. Social proximity in an ungulate expressed as frequency and duration of interactions. Canadian Journal of Zoology.

Fox, C.H., R. El-Sabaawi, P.C. Paquet, and T.E. Reimchen. 2014. Pacific herring (*Clupea pallasii*) and wrack macrophytes subsidize semi-terrestrial detritivores. Marine Ecology Progress Series.

Adams, M. S., J. Carpenter, J. A. Housty, D. Neasloss, P. C. Paquet, C. Service, J. Walkus, and C. T. Darimont. 2014. Toward increased engagement between academic and indigenous community partners in ecological research. *Ecology and Society* **19**(3): 5.
http://dx.doi.org/10.5751/ES-06569-190305

Artelle, K.A., Reynolds, J.D. Paquet, P.C. & Darimont, C.T. 2014. When science-based management isn't. *Science* **343**, 1311.

Darimont, C.T., C. Genovali, C. Service, and P.C. Paquet. In Press. Hunting for a trophy hunting ethic. In *Animals and the Environment: Advocacy, Activism, and the Quest for Common Ground (L. Kemmerer, Ed).* Routledge Press.

Bryan, H.M., Darimont, C.T., Paquet, P.C., Wynne-Edwards, K.E., and Smits, J.E.G. 2014. Stress and reproductive hormones reflect inter-specific social and nutritional conditions mediated by resource availability in a bear-salmon system. Conservation Physiology 2(1): cou010doi: 10.10 93/conphys/cou010

Stronen, A.V., Navid, E.L., Quinn, M.S., Paquet, P.C., Bryan, H.M., and Darimont, C.T. 2014. Population genetic structure of gray wolves (*Canis lupus*) in a marine archipelago suggests island-mainland differentiation consistent with dietary niche. BMC Ecology 14:11. doi:10.1186/1472-6785-14-11

Christina N. Service, Megan S. Adams, Kyle A. Artelle, Laura V. Grant, Paul C. Paquet, and Chris T. Darimont. 2014. Indigenous knowledge and science unite to reveal spatial and temporal dimensions of distributional shift in wildlife of conservation concern. PLOS ON DOI: 10.1371/journal.pone.0101595

Bryan, Heather M., Judit E. G. Smits, Lee Koren, Paul C. Paquet, Katherine E. Wynne-Edwards and Marco Musiani. 2014. Heavily hunted wolves have higher stress and reproductive steroids than wolves with lower hunting pressure. Functional Ecology. DOI: 10.1111/1365-2435.12354

Brook, R.K., Cattet, M., Darimont, C.T., Paquet, P.C. and G. Proulx. 2015. Maintaining ethical standards during conservation crises. *Canadian Wildlife Biology & Management* 4: 72-79.

Fox, C.H., Paquet, P.C., and T.E. Reimchen. 2015. Novel species interactions: American black bears respond to Pacific herring spawn. BMC Ecology. DOI 10.1186/s12898-015-0045-9.

Best, B.D., Fox, C.H., Williams, R., Halprin, P.N., and P.C. Paquet. 2015. Updated marine mammal distribution and abundance estimates in British Columbia. Journal Of Cetacean Research and Management. 15: 9–26.

Cullingham, C.I., Thiessen, C.D., Derocher, A.E., Paquet, P.C., Miller, J.M., Hamilton, J.A., and D.W. Coltman. 2016. Population structure and dispersal of wolves in the Canadian Rocky Mountains. Journal of Mammalogy. DOI: http://dx.doi.org/10.1093/jmammal/gyw015

Caroline H. Fox, Aerin L. Jacob, Chris T. Darimont, Paul C. Paquet. 2016. Pacific herring and fisheries management in Canada: A new era or repeated history?, Ocean & Coastal Management. 125: 47-48, ISSN 0964-5691, http://dx.doi.org/10.1016/j.ocecoaman.2016.03.004.

Artelle, K.A., Anderson, Reynolds, J.D., Cooper, A.B., Paquet, P.C., and C.T. Darimont. 2016. Ecology of conflict: marine food supply affects human-wildlife interactions on land. Sci. Rep. 6, 25936; doi: 10.1038/srep25936.

C.H. Fox, P.D. O'Hara, S. Bertazzon, K. Morgan, F.E. Underwood, P.C. Paquet. 2016. A preliminary spatial assessment of risk: Marine birds and chronic oil pollution on Canada's Pacific coast. Science of The Total Environment. 573: 799-809, ISSN 0048-9697, http://dx.doi.org/10.1016/j.scitotenv.2016.08.145.

Fox, C.H., Huettmann, F., Morgan, K., O' Hara, P., Paquet, P.C. 2017. Predictions from Machine Learning ensembles: marine bird distribution and density on Canada's Pacific coast. Marine Ecology Progress Series. Vol. 566: 199–216, 2017 doi: 10.3354/meps12030

Proulx, G., Alexander, S., Barron, H., Bekoff, M., Brook, R., Bryan, H., Darimont, C., Dubois, S., Lukasik, V., McCrory, W., Paquet, P., Parr, S., Powell, R. Vik Sronen, A., and A. Wallach. 2017. Killing wolves and farming caribou benefit industry, not caribou: a response to Stan Boutin. Nature Alberta Volume 47, Number 1, pages 4-11

Adams, M. S., C. N. Service, A. Bateman, M. Bourbonnais, K. A. Artelle, T. Nelson, P. C. Paquet, T. Levi, and C. T. Darimont. 2017. Intrapopulation diversity in isotopic niche over landscapes: Spatial patterns inform conservation of bear–salmon systems. Ecosphere 8(6):e01843. 10.1002/ecs2.1843

Harvey, G. K. A., T. A. Nelson, C. H. Fox, and P. C. Paquet. 2017. Quantifying marine mammal hotspots in British Columbia, Canada. Ecosphere 00(00):e01884. 10.1002/ecs2.1884

Lacy, R. C., R. Williams, E. Ashe, K. C. Balcomb III, L. J. N. Brent, C. W. Clark, D. P.

Croft, D. A. Giles, M. MacDuffee, and P. C. Paquet. 2017. Evaluating anthropogenic threats to endangered killer whales to inform effective recovery plans. Scientific Reports **7**:14119.

Treves, A., K. A. Artelle, C. T. Darimont, W. S. Lynn, P. Paquet, F. J. Santiago-Ávila, R. Shaw, and M. C. Wood. 2018. Intergenerational equity can help to prevent climate change and extinction. Nature Ecology & Evolution **2**:204-207.

Darimont, C. T., P. C. Paquet, A. Treves, K. A. Artelle, and G. Chapron. 2018. Political populations of large carnivores. Conservation Biology, Volume 32: 747–749. DOI: 10.1111/cobi.13065

K. A. Artelle, J. D. Reynolds, A. Treves, J. C. Walsh, P. C. Paquet, C. T. Darimont, Hallmarks of science missing from North American wildlife management. Sci. Adv. 4, eaao0167 (2018). DOI: https://doi.org/10.1126/sciadv.aao0167

C. H. Fox, P. C. Paquet, T. E. Reimchen. 2018. Pacific herring spawn events influence nearshore subtidal and intertidal species. MEPS https://doi.org/10.3354/meps12539

Hendricks, S., R. Schweizer, R. Harrigan, J. Pollinger, R. Brown, P. Paquet, C. Darimont, J. Adams, L. Waits, B. vonHoldt, P. Hohenlohe, and R. Wayne. In Press 2018. Natural re-colonization and admixture of wolves (*Canis lupus*) in the US Pacific Northwest: challenges for the protection and management of rare and endangered taxa. Heredity. https://doi.org/10.1038/s41437-018-0094-x

Batavia C, Nelson MP, Darimont CT, Paquet PC, Ripple WJ, Wallach AD. The elephant (head) in the room: A critical look at trophy hunting. Conservation Letters.2018;e12565. https://doi.org/10.1111/conl.12565

K.A. Artelle, J.D. Reynolds, A.Treves, J.C. Walsh, P.C. Paquet, C.T. Darimont. 2018. Working constructively toward an improved North American approach to wildlife management. Sci Adv 4 (10), eaav2571. DOI: 10.1126/sciadv.aav2571

Treves, A., Artelle, K.A., and P.C. Paquet. 2018. Differentiating between regulation and hunting as conservation interventions. Conservation Biology.
DOI:10.1111/cobi.13211

Paquet, P.C. and Alexander, S.M. 2018. Habitat loss: changing how animals think? Pages 4-14 *In* Andrew Butterworth, editor. Animal welfare in a changing world. 2018. CABI Wallingford, Oxfordshire, UK; Boston, MA. LC record available at https://lccn.loc.gov/2017059470

Service, C. et al. In press. Salmonid species diversity predicts salmon consumption by terrestrial wildlife. Journal of Animal Ecology

Peer Reviewed Books and Chapters

Harrington, F.H. and P.C. Paquet (Eds.). 1982. Wolves of the world: Perspectives of behavior, ecology, and conservation. Noyes Publications, New Jersey

Harrington, F.H. and P.C. Paquet (Eds.). 1982. Wolves of the world: Perspectives of behavior, ecology, and conservation. 2nd edition. Noyes Publications, New Jersey

Paquet, P.C., S. Bragdon, and S. McCusker. 1982. Cooperative rearing of simultaneous litters in captive wolves. In F.H. Harrington and P.C. Paquet (Eds.) Wolves of the World, Noyes Publications, New Jersey, p. 223-237.

Harrington, F.H., P.C. Paquet, J. Ryon, and J.C. Fentress. 1982. Monogamy in wolves: A review of the evidence. In F.H Harrington and P.C Paquet (Eds.) Wolves of the World, Noyes Publications, New Jersey, p. 209-222.

Paquet, P.C. and W.A. Fuller. 1990. Scent marking and territoriality in wolves of Riding Mountain National Park. In Chemical signals in vertebrates 5. Eds. D.W. Macdonald, D. Muller-Schwarze, and S.E. Natynczuk. Oxford University Press, N.Y. pp 394-400.

Boyd, D.K., Paquet, P.C., Donelon S., Ream, R.R., Pletscher, D.H., and C.C. White. 1995. Transboundary movements of a recolonizing wolf population in the Rocky Mountains. Pages 135-140 In L.N. Carbyn, S.H. Fritts, and D.R. Seip, editors, Ecology and conservation of wolves in a changing world. Canadian Circumpolar Institute, Edmonton, Alberta.

Woods, J., Cornwell, L.L., Hurd, T., Kunelius, R., Paquet, P., and J. Wierzchowski 1996. Elk and Other Ungulates. Chapter 8 in: Green J., Pacas, C, Bayley, S., and Cornwell, L. (eds). A cumulative effects assessment and futures outlook for the Banff Bow Valley. Prepared for the Banff Bow Valley Study, Department of Canadian Heritage, Ottawa, On.

Paquet, P.C., Wierzchowski, J. and Callaghan, C. 1996. Summary report on the effects of human activity on gray wolves in the Bow River Valley, Banff National Park, Alberta. Chapter 7 in: Green J., Pacas, C, Bayley, S., and Cornwell, L. (eds). A cumulative effects assessment and futures outlook for the Banff Bow Valley. Prepared for the Banff Bow Valley Study, Department of Canadian Heritage, Ottawa, On.

Paquet, P.C., and C. Callaghan. 1996. Effects of linear developments on winter movements of gray wolves in the Bow River Valley in Banff National Park, Alberta. Pages 46-66 In G.L. Evink, P. Garrett, D. Ziegler, and J. Berry, editors. Trends in Addressing Transportation Related Wildlife Mortality. Proceedings of the Transportation Related Wildlife Mortality Seminar. FL-ER-58-96. Florida Department of Transportation, Tallahassee, Florida, U.S.A.

Paquet, P.C. and Callaghan, C. 1997. GIS decision support models for highway planning. In G. Evink, D. Ziegler, P. Garret, and J. Barry, editors, Highways and movements of wildlife: improving habitat connections and wildlife passageways across highway corridors. Proceedings of the Florida Department of Transporation/Federal Highway Administration Transportation-Related Wildlife Mortality Seminar.

Terborgh, J., Estes, J.A., P.C. Paquet, K, Ralls, D. Boyd-Heger, B.J. Miller, and R.F. Noss. 1999. The role of top carnivores in regulating terrestrial ecosystems. Pages 39-64 in Continental Conservation, eds. M.E. Soule and J. Terborgh. Island Press, Washington, D.C. 227pp.

Carroll, C., Noss, R.F., Shoemaker, N, and P.C. Paquet. 2001. Is the restoration of wolf, wolverine, and grizzly bear to Oregon and California biologically feasible? In D. S. Maeher, R. F. Noss, and J. L. Larkin (eds.) Large Mammal Restoration, Island Press, Washington, D.C.

Duke, D.L., Hebblewhite, M., Paquet, P.C., Callaghan, C., and M. Percy. 2001. Restoration of a large carnivore corridor in Banff National Park, Alberta. Pages 261-276 in D. S. Maeher, R. F. Noss, and J. L. Larkin (eds.) Large Mammal Restoration, Island Press, Washington, D.C..

Paquet, P.C., J. R. Strittholt, N. L. Staus, P. J. Wilson, S. Grewal, and B. N. White. 2001. Feasibility of timber wolf reintroduction in Adirondack Park. Pages 47 - 64, in D. S. Maeher, R. F. Noss, and J. L. Larkin (eds.). Large Mammal Restoration, Island Press, Washington, D.C.

Paquet, P.C. 2001. Wolves. Pages 42-45, In D. Macdonald (ed) New Encyclopedia of Mammals, Oxford University Press, Oxford.

Paquet, P.C. 2001. An ongoing genetic mystery. Pages 46-47, in D. Macdonald (ed) New Encyclopedia of Mammals, Oxford University Press, Oxford.

Alexander, S., N. Waters, and P.C. Paquet. 2002. A Uncertainty-Based Decision Support Model for Restoring Wildlife Landscape Connectivity in Road

Fragmented Environments. In G. Clarke and J. Stillwell, editors. Applied GIS and Spatial Modelling. University of Leeds, United Kingdom.

Paquet, P. C. and L. N. Carbyn. 2003. Wolf, Canis lupus and allies. Pages 482-510 in G. A. Feldhamer, B. C. Thompson, and J. A. Chapman, editors. Wild Mammals of North America: Biology, Management, and Conservation. Johns Hopkins University Press, Baltimore, MD

Alexander, S., N. Waters, and P.C. Paquet. 2004. A Probability-based GIS Model for Identifying Focal Species Linkage Zones across Highways in the Canadian Rocky Mountains. Pages 233-255 in G. Clarke and J. Stillwell, editors. Applied GIS and Spatial Modelling. University of Leeds, United Kingdom.

Paquet, P. C., S. M. Alexander, P. L. Swan, and C. T. Darimont. 2006. Pages 130-156 in Connectivity Conservation, eds K. R. Crooks and M. Sanjayan. Influence of natural landscape fragmentation and resource availability on distribution and connectivity of marine gray wolf (*Canis lupus*) populations on Central Coast, British Columbia, Canada. Cambridge University Press. N.Y. & England.

Paquet, P.C., S.M. Alexander, P.L. Swan, and C.T. Darimont. 2006. The influence of natural landscape fragmentation and resource availability on connectivity and distribution of marine gray wolf populations on the Central Coast, British Columbia, Canada. In Crooks, K. and M.A. Sanjayan (Eds.) Connectivity Conservation. Cambridge University Press. Cambridge, UK.

Paquet, P.C. Introduction. In McAllister, I., and C.T. Darimont. 2007. The Last Wild Wolves. Ghosts of the Great Bear Rainforest. University of California Press. Berkeley, CA.

Musiani, M., Boitani, L. and P. C. Paquet (eds.). 2009. A New Era for Wolves and People: Wolf Recovery, Human Attitudes, and Policy. University of Calgary Press, Calgary. AB Canada.

Bloch, G. , Dettling, P., Paquet, P. C., Gibeau, M. 2009. Auge in Auge mit dem Wolf. Kosmos, Koln, Germany.

Musiani, M, Boitani, L, and P. C. Paquet (eds.). 2010. The world of wolves: new perspectives on ecology, behaviour and policy. University of Calgary Press, Calgary. AB, Canada.

Musiani, M, Boitani, L, and P. Paquet (eds). 2010. A new era for wolves and people: wolf recovery, human attitudes and policy. University of Calgary Press, Calgary. AB, Canada.

H. Dean Cluff, H.D., Paquet, P.C., Walton, L.R., and M. Musiani. 2010. Wolf Ecology and Management in Northern Canada: Perspectives from a Snowmobile Wolf Hunt. In Musiani, M, Boitani, L, and P. Paquet (eds) The world of wolves: new perspectives on ecology, behaviour, and policy. University of Calgary Press, Calgary. AB, Canada.

Paquet, P.C., Alexander, S., Donelon, S., and C. Callaghan. 2010. Influence of anthropogenically modified snow conditions on movements and predatory behaviour of gray wolves. In Musiani, M, Boitani, L, and P. Paquet (eds) The world of wolves: new perspectives on ecology, behaviour, and policy. University of Calgary Press, Calgary. AB, Canada

Paquet, P.C., Miller, B., Kunkel, K., Reading, R.P., and M.K. Phillips. 2010. The importance of large carnivores. Pages 49-60 in Reading, R.P., B. J. Miller, A. Masching, R. Edward, and M. Phillips (eds.). Awakening Spirits: Wolves in the Southern Rockies. Fulcrum Publishing, Golden, CO.

Phillips, M.K. Miller, B., Kunkel, K., Paquet, P.C., Martin, W.W. and D.W. Smith. Potential for and implications of wolf restoration in the Southern Rockies. 2010. Pages 197-218 in Reading, R.P., B. J. Miller, A. Masching, R. Edward, and M. Phillips (eds.). Awakening Spirits: Wolves in the Southern Rockies. Fulcrum Publishing, Golden, CO.

Paquet, P.C. 2010. Foreword in Dettling, P. Will of the Land. Rocky Mountain Press. Canmore, AB.

DellaSala, D., Moola, F., Paquet, P., Noss, R. 2011. North America Coastal Rainforest: Alaska to the Redwoods. In DellaSala, D. (ed). Temperate and Lesser Known Rainforests of the World: Their Ecology and Conservation. Island Press

DellaSala, D., Paquet, P., McClellan, B., Alaback, P., Goward, T., Craighead, L. and T. Spribille. 2011. Inland Temperate Rainforests of the Interior Northwest. In DellaSala, D. (ed). Temperate and Lesser Known Rainforests of the World: Their Ecology and Conservation. Island Press

DellaSala, D.A., Alaback, P., Kirkpatrick, J., Paquet, P., von Wehrden, H., Techlin, D., Krestov, P., Noss, R., Hakon, H., Craighead, L., Nakamura, Y., Moola, F., Nauman, R., and T. Spribille. 2011. Rainforests at the brink: A call for international action. In DellaSala, D. (ed). Temperate and Lesser Known Rainforests of the World: Their Ecology and Conservation. Island Press

2011. Crosscutting Issues and Conservation Strategies. In DellaSala, D. (ed). Temperate and Lesser Known Rainforests of the World: Their Ecology and Conservation. Island Press.

Paquet, P.C. (guest statement). The Role of Traditional Ecological Knowledge in Conservation *in* Alexander, S.M. 2015. Carnivore Management and the Role of Conservation GIS. Chapter 13 (Pages 293-317) *in* Resources and the Environmental Management in Canada, 5th Ed., Mitchell, B., Ed. Oxford University Press. Pages 308-309.

Darimont, C., Artelle, K., Bryan, H., Genovali, C., MacDuffee, M., and P. Paquet. 2015. Brown bears, salmon, people: travelling upstream to a sustainable future. Chapter 14 *in* Bear Necessities, rescue, rehabilitation, sanctuary, and advocacy (Kemmerer, L., Ed.). Brill, Boston, U.S.A. Pages 149-164.

Paquet, P.C. and Alexander, S.M. 2018. Habitat loss: changing how animals think? Pages 4-14 *In* Andrew Butterworth, editor. Animal welfare in a changing world. 2018. CABI Wallingford, Oxfordshire, UK; Boston, MA. LC record available at https://lccn.loc.gov/2017059470

Peer reviewing

I review ≥10 submissions per year, including those made to the following Journals: Biology Letters, Oikos, Oecologia, Animal Conservation, Aquatic Biology, Journal of Applied Ecology, Functional Ecology, Animal Behaviour, Marine Ecology Progress Series, Conservation Biology, Journal of Mammalogy, Behavioral Ecology, Biological Conservation, Rangifer, Northeastern Naturalist, Wildlife Biology.

Areas of Expertise

- Environmental Ethics
- Large Carnivores
- Predator Prey Relationships
- Population Ecology & Wildlife Disease
- Population Dynamics of Large Mammals
- Habitat Analysis
- Computer Modelling
- Telemetry
- Remote Sensing Techniques
- GIS applications
- Live Capture and Immobilization of Carnivores

Additional Interests and Skills

- Photography
- Auto Mechanics
- Mountaineering
- Carpentry

Misty MacDuffee, C.V.
2621 Chart Drive, Pender Island, BC V0N 2M1
250.629.3001
misty@raincoast.org

Introduction

I am a conservation biologist with a focus on fisheries ecology in salmon ecosystems. For the past 15 years I have undertaken various types of field, laboratory, technical and conservation assessments in the salmon-bearing watersheds of the BC coast. I have a particular interest in the role of salmon as critical food sources for wildlife and incorporating their nutritional and energetic needs into salmon management decisions. I am also interested in historic stock assessment and run reconstructions in salmon watersheds. The application of my work is to implement ecosystem considerations in fisheries management. This often requires my engagement with management, dialogue and stakeholder forums that affect fisheries and wildlife policy and management.

Education

Bachelor of Science

2002-2006 Biology, University of Victoria, Victoria, British Columbia,
1982-1985 Environmental Science and Environment Studies, Trent University, Peterborough, Ontario

Work History

2005- current Conservation Biologist, Raincoast Conservation Foundation (RCF)
Program Focus: Sustainable fisheries and conservation of salmon ecosystems

- Salmonid inventories and status assessments
- Juvenile salmon field assessments of presence/absence, habitat indicators and use
- Fish community assessments in river, estuarine and marine ecosystems
- documentation/characterization of grizzlies diets and salmon use by grizzlies
- Examining the role of salmon nutrients to sockeye nursery lake production
- Use of paleolimnological tools to understand past trends and drivers (nutrients, climate, harvest) in sockeye abundance, productivity and population dynamics.
- Examination of stock recruitment models as appropriate management tools to meet objectives under Canada's Wild Salmon Policy.

2014- Present Naturalist and Guide, Maple Leaf Adventures

- Guiding and interpreting wildlife and natural history on BC's south, central and north coast with focus on toothed and baleen whales, birds, grizzlies and salmon

August 2010 - November 2010 Team Leader: Salmon enumeration/creek walker. Mainland Enhancement Salmonid Society, subcontract to Fisheries and Oceans Canada

- In-stream (live) enumeration and carcass counts of salmon species in 15 streams and rivers of the Broughton Archipelago
- Determining and assessing juvenile salmon presence and distribution
- Collection of tissues for molecular genetic analysis
- Stream and watershed reviews and recommendations for improved habitat conservation

Fall 2008. Salmon enumeration and creek walker. Sub contract to Simon Fraser University.

- In-stream (live) enumeration and carcass counts of salmon species in a dozen streams and rivers within Fisheries Management Area 7 on BC central coast.

Summers 2004-2006. Platform Observer and crew, Marine Mammal At- Sea Surveys, RCF

- Observation and identification of cetaceans and pinnipeds (whales, dolphins, seals, sea lions) from boat-based line transect surveys throughout the Queen Charlotte Basin.

1996 - 2002 Salmon Ecologist & Community Advisor, Institute of Ocean Sciences & University of Victoria

- Restoration elements of degraded freshwater and marine salmonid habitats including stream, watershed, hydrologic, near shore and foreshore assessments,
- salmonid assessments and stock assessment,
- habitat prescriptions and recommendations to governments and community agencies on improving freshwater and marine aquatic conditions for salmonids and other organisms.

Field Skills

- 20 years experience operating small boats and zodiacs on the BC coast,
- SVOP certification and Marine Radio Operators license
- Marine Emergency Duties MED A1, A2 and A3 certification
- Red Cross Advanced Marine First Aid and Advanced Wilderness First Aid
- PADI open water diver certification
- Assistant bear-viewing guide certification with Commercial Bear Viewing Association
- Class 5 drivers license and extensive experience driving trucks and trailers
- have lead my own field research programs and crewed for others
- have sampled, collected, assessed and inventoried abiotic and biotic features of remote coastal regions
- can work safely and independently with wildlife and have been responsible for safety of others

Scientific Published Papers

Chalifour, L., D.C. Scott, **M. MacDuffee,** J.C. Iacarella, T.G. Martin and J.K. Baum. *2019.* Habitat selectivity by juvenile salmon, resident and migratory species underscores the importance of estuarine habitat mosaics. *In review*

Gayeski, Nick, **Misty MacDuffee**, and Jack A. Stanford. 2018. Criteria for a Good Catch: A Conceptual Framework to Guide Sourcing of Sustainable Salmon Fisheries. *Facets.* 3: 300–314. https://doi.org/10.1139/facets-2016-0078

Kehoe, L.J., J.Lund, L. Chalifour, J.M. Casey, B. Connors, N. Cryer, M.C. Drever, C. Levings, **M. MacDuffee,** H. McGregor, D.C. Scott, R.G. Vennesland, C.E. Wilkinson, P. Zevit, J.K. Baum and T.G. Martin. *in review.* Prioritizing conservation action in a highly contested socio-ecological system.

Lacy, Robert C., R. Williams, E. Ashe, K.C. Balcomb III, L.J. N. Brent, C.W. Clark, D.P. Croft, D.A. Giles, **M. MacDuffee** and P.C. Paquet. 2017. Evaluating anthropogenic threats to endangered killer whales to inform effective recovery plans. *Scientific Reports.* 7, Article number: 14119 doi:10.1038/s41598-017-14471-0

Michael H.H. Price, K.K. English, A.G. Rosenberger, **M. MacDuffee,** and J.D. Reynolds. 2017. Canada's Wild Salmon Policy: an assessment of conservation progress in British Columbia. *Can J. Fish & Aquatic Sci.* https://doi.org/10.1139/cjfas-2017-0127

Jarvela Rosenberger, A.L., **M.MacDuffee,** A.G. J. Rosenberger and Peter S. Ross. 2017. Oil Spills and Marine Mammals in British Columbia, Canada: Development and Application of a Risk-Based Conceptual Framework. *Archives of Environmental Contamination and Toxicology* 73: 131. https://doi.org/10.1007/s00244-017-0408-7

Darimont, C.T., K. Artelle, H. Bryan, C. Genovali, **M. MacDuffee**, and P.C. Paquet. 2013. Brown bears, salmon, people: Traveling upstream to a sustainable future. Chapter 14 *in* Bear Necessities: Rescue, Rehab, Sanctuary and Advocacy. Lisa Kemmerer *ed.* Brill Press. Boston

Christensen, J.R., M.B. Yunker, **M. MacDuffee** and P.S. Ross. 2013. Plant consumption by grizzly bears reduces biomagnification of salmon-derived PCBs, PBDEs, and organochlorine pesticides. *Env.Tox. Chem.* 02/2013

Levi T., C.T. Darimont, **M. MacDuffee,** M. Mangel, P. Paquet, C.C Wilmers. 2012. Using Grizzly Bears to Assess Harvest-Ecosystem Tradeoffs in Salmon Fisheries. *PLoS Biol* 10(4)

Darimont, C.T., Bryan, H.M., Carlson, S.M., Hocking, M.D., **MacDuffee, M.**, Paquet, P.C., Price, M.H.H., Reimchen, T.E., Reynolds, J.D., and Wilmers, C.C. 2010. Salmon for terrestrial protected areas. *Conservation Letters.* 3(6): 379–389

MacDuffee, M. and E. MacIsaac (eds). 2009. Applications of paleolimnology to sockeye salmon nursery lakes and ecosystems in the Pacific Northwest and Alaska: Proceedings of a workshop at the Institute of Ocean Sciences, October 2008. *Can. Tech. Rep. Fish. Aquat. Sci.* No. 2847

Price, M.H., C.T. Darimont, N.F. Temple and **M. MacDuffee.** 2008. Ghost Runs: Management and status assessment of Pacific salmon returning to British Columbia's central and north coasts. *Can. J. Fish. Aquat. Sci.* Vol 65, No 12, pp. 2712-2718(7)

Christensen, J.R., **MacDuffee, M**., Yunker, M.B., and Ross, P.S. 2007. Hibernation associated changes in persistent organic pollutants (POP) levels and patterns in British Columbia grizzly bears. *Environ.Sci.Technol.* 41: 1834 - 1840;

Christensen, J.R., **MacDuffee, M**., MacDonald, R.W., Whiticar, M. and Ross, P.S. 2005. Persistent Organic Pollutants in British Columbia's Grizzly Bears: Consequence of Divergent Diet. *Environ. Sci. Technol.* 39: 6952-6960

Expert Reports for Legal Proceedings

December 2011. Written evidence of Misty MacDuffee on the marine risks and impacts to British Columbia's wild salmon. Submitted to Canada's CEAA-NEB Joint Review Panel in the matter of Enbridge's Northern Gateway Environmental and Socio-economic Assessment.

May 2015. Written evidence of Kate Logan, Dave Scott and Misty MacDuffee on Potential Effects on Fraser River Salmon from an oil spill by the Trans Mountain Expansion Project. Submitted to National Energy Board in the matter of Trans Mountain ULC Environmental Assessment.

July 2013. Written evidence of Misty MacDuffee on the conservation status of British Columbia's south coast salmon populations. Submitted to the federal court in the matter of Morton vs. Fisheries and Oceans Canada and Marine Harvest.

Past Positions and Committees

2009 - current Marine Conservation Caucus representative to Fisheries & Oceans Canada's Integrated Harvest Planning Committee (IHPC) for salmon fisheries

2012 – current Marine Conservation Caucus representative to Fisheries & Oceans Canada Technical Working Group to the Southern BC Chinook Strategic Planning Initiative

2018 – current Marine Conservation Caucus representative to Fisheries & Oceans Canada Southern Resident killer whale Prey Working Group

2018 – current Member of Fisheries & Oceans Canada's Southern Resident killer whale Stakeholder Working Group

2008 - current Raincoast Conservation Foundation representative to BC's Marine Conservation Caucus

2007- 2012 Committee member, Rivers Inlet Recovery Team/ Rivers-Smith Salmonid Ecosystem Society

2009 - 2011, Chair, Board of Directors, Gulf Islands Alliance

2011- 2017, Director, Gulf Islands Alliance

1999 - 2006 Chair, Board of Directors, Raincoast Conservation Foundation