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by

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ABSTRACT

We evaluate the current commercial harvest of harp seal (*Pagophilus groenlandicus*) and proposed subsistence harvests of northern fur seal (*Callorhinus ursinus*) pups based on intra-specific comparisons. These comparisons utilize a pattern derived from 167 cases of estimated consumption rates by large mammals. In all cases, the predation rates involve large mammal prey less than 1 year of age. Recent harvests of harp seal pups are exceeded by 20 (about 12%) of the estimated consumption rates among the nonhuman species. Although this is not statistically significant, further analysis may find this harvest to be unsustainable when we account for other factors such as the number of other predators, the number of prey each predator consumes, trophic level, the biodiversity of the system, and differences involving terrestrial predators preying on marine prey.

Initially, there is no scientific basis for rejecting a proposed subsistence harvest of 150 northern fur seal pups on St. George Island, Alaska, or a comparable harvest of 1,125 pups on St. Paul Island. The proposed harvests of fur seal pups are exceeded by 162 (97%) of the 167 cases of predation among nonhuman predatory species. In both cases, therefore, the harvests represent consumption rates in the lower extremes of predation rates observed for nonhuman species. Further explicit consideration of relevant factors could lead to a slight reduction in the assurance that the harvest of 150 pups is sustainable, but there is a low likelihood that such a harvest would prove to be unsustainable. This determination accounts for the complexity of the ecosystems involved owing to the integrative nature of the patterns used in the evaluation. The northern fur seal population is declining, raising concerns about the addition of a subsistence harvest to the mortality this species experiences. In management, a declining population reflects all of the

contributing factors to include all human influence. Management is necessary to relieve systems of the abnormal effects of our activities whenever human influence is found to be unusual, abnormal, or pathological. Such influence involves the full spectrum of human activities to include the effects of abnormal fisheries harvests, pollution, and CO₂ production. As long as harvests of the declining species are not abnormally large, other abnormal human influences are the preferred focus of management.

The comparisons used in our study make the conclusions regarding northern fur seals seem conservative, largely because most examples of predation among nonhuman predators exceed the harvest rates proposed for this species. Overtly accounting for other factors could lead to the conclusion that proposed harvests are less conservative than initially indicated. We show, for example, that directly accounting for the number of competing predators is likely to show the proposed harvest to be exceeded by a smaller portion of the sample among nonhuman predators than when this factor is not explicitly treated. Nevertheless, the mortality rates of the proposed harvest are small enough that it is likely that they fall in the lower end of the spectrum of most subsets of data for consumption rates among other large mammals – subsets that would emerge through explicit consideration of more specific management questions.

INTRODUCTION

The harvest of young-of-the-year from large mammal populations (by humans) is exemplified by the commercial take of the phocid harp seals (*Pagophilus groenlandicus*) in the northwest Atlantic. From a single species perspective, one of the questions facing managers in cases like these is: *At what rate can we sustainably harvest harp seals?* More specifically, the question might be: *What portion of the pup production by harp seals can be harvested sustainably?* From the ecosystem perspective, the complimentary question is: *What portion of the pup production by harp seals should be left unharvested to sustainably preserve the natural dynamics of the population of their species and the characteristics of their ecosystem?* (Hobbs and Fowler 2008). Conventionally, pup harvests would be addressed using models of 'surplus production', 'maximum sustainable yield', or 'potential biological removal'. Such approaches are simplistic, misleading, often result in overharvesting, and, like all management, lead to unintended effects on ecosystems. All harvesting has genetic effects on the resource species – many of which are judged to be negative or undesirable. How can management be carried out to account for such factors?

Pups of the northern fur seal (*Callorhinus ursinus*), have been harvested by the indigenous people of North America for centuries (Etnier 2002). In the spirit of cultural tradition, the community of St. George Island, Alaska, has proposed that their residents be allowed an annual take of 150 male northern fur seal pups. This harvest would be taken from about 17,000 pups of both sexes currently born on this island each year (Towell et al. 2006). It is now possible to evaluate the sustainability of various levels of take from any large mammal population by comparing harvests to patterns in consumption observed among other predatory

species (Fowler and Hobbs 2002, Belgrano and Fowler 2008). This involves implementation of the principles of management (embodied in systemic management, Fowler 2003).

Here we evaluate three harvests: 1) the harvest of harp seal pups in the northwest Atlantic, 2) the proposed harvest of northern fur seal pups on St. George Island, Alaska, and 3) a hypothetical harvest of northern fur seal pups on St. Paul Island comparable to that proposed for St. George (the latter two islands are the two largest in the Pribilof Archipelago in the Bering Sea where the largest portion of the global population of northern fur seals breed). These evaluations are based on comparisons with observed consumption rates by other large mammal predators in their take of juveniles (less than 1 year of age) from large mammal populations. The choice of these sets of comparisons overtly accounts for the *a priori* knowledge that the predator and prey (humans and fur/harp seals) are both large mammals and that the prey are young-of-the-year. Our analyses of these data exemplify part of the decision-making process in systemic management: the process of directly accounting for factors such as number of predatory species, body size, taxonomic status, and trophic level. More specific comparisons will have to await the results of research to provide information that is missing in current data: other knowledge of these or similar systems. The need for research is defined by the management question being addressed as explained in the discussion section below, with examples. Refining such questions (asking more specific management questions) leads to defining further research.

METHODS

The literature on predator/prey relationships was searched for information regarding the predation rate of large mammal predators on large mammal prey (from about 5.5 kg to about

600 kg adult body size for predators, and from 50 kg to 525 kg as the adult body size for the prey species), specifically where the prey taken were less than 1 year of age. This choice was based on the objective of achieving a match or consonance¹ between management question and the pattern used for evaluation or establishing management advice (Belgrano and Fowler 2008). The question (e.g., *At what rate can we sustainably harvest harp seal [or fur seal] pups?*) inherently specifies humans as the predator and seals as the prey; in each case, both are large mammals. We achieve a match between information and management question when the data used in management involves predation patterns that are specific to large mammals in both cases. In addition to body size, the question specifies pups or young-of-the-year; thus, the data we examined were restricted to young-of-the-year for the prey – continuing to maintain the match.

Predation rates were recorded for each study as reported in the literature, each rate specific to the time period covered by the study. Some studies were designed and carried out over a full year; others were shorter studies that resulted in estimates of mortality pertinent to only several months. Percentages were converted to portions; thus, a mortality rate of 15% was recorded as a crude mortality rate of $M = 0.15$.

¹Consonance involves the mapping of management question to pattern developed in scientific research. A pattern fully consonant with the management question occurs when the pattern and question involve completely identical units of measure, are of identical logical type, and are perfectly isomorphic. There is a one-to-one mapping from question to pattern (Belgrano and Fowler 2008).

The number of predatory species reported to be involved in the overall mortality of juveniles in each case was also recorded (when available), in addition to the predation rates recorded for specific predators.

Scientific names were recorded as they were used in the original source documents. This means that some of the names used in our results may be outdated by current taxonomic standards.

Cannibalism was not considered to be predation because the management question being addressed involves the sustainable consumption of one prey species by a predatory species that is different from the prey (using data on cannibalism would result in a mismatch with the management question because cannibalism involve one species eating individuals of same species). The predatory species about which the management question is being posed is the human species, *Homo sapiens*. Asking the management question (in the case of northern fur seals: *At what rate can we sustainably harvest northern fur seal pups for human consumption?*) that specifies humans as the consumer follows an important tenet of management. This tenet requires that management be intransitive in regulating or controlling our (human) interactions with other natural systems, in this case another species (Fowler 2003).

Predation rates by the domestic dog were included, as were predation rates estimated for unidentified species thought to be large mammals.

Male and female prey were not distinguished; for this study the predation rates were assumed to apply to the 0-1 year-old age class without regard to sex.

The harvests of harp seals and proposed harvests of fur seals were converted to mortality rates expressed in the units reported in the literature for nonhuman predators. The proposed (or

comparable) harvests of northern fur seal pups was divided by the estimated population size of the newborn portion of the population for each island (17,000 for St. George, and 122,000 for St. Paul; Towell et al. 2006) to find the crude mortality rate (M). For example, M for the requested harvest on St. George was calculated as $150/17,000 = 0.00824$ (= 0.8824%). All crude annual mortality rates were converted to \log_{10} scale for comparison with mortality rates similarly calculated for the nonhuman predators from the literature used in this study. These conversions preserved matching units as required of systemic management so that, in application, no conversion is required of, or allowed by, stakeholders (Belgrano and Fowler 2008).

The human population on St. George is about 100 and on St. Paul the human population was assumed to be about 750 (it is probably actually closer to 500 with a 'native' component of about 85%). A harvest on St. Paul comparable to the proposed harvest on St. George would, under the assumption of a human population of 750, be approximately 1,125 pups. This converts to an estimated crude mortality rate of 0.92% ($M = 1,125/122,000 = 0.0092$). Various harvest rates were used for each Pribilof island to evaluate alternatives that covered a span of values inclusive of these harvest levels and their corresponding mortality rates. A minimum of 500 fur seal pups was used in the harvest options evaluated for St. Paul; the minimum we used for St. George was 50 pups. The maximum evaluated in each case was the harvest corresponding to the mean consumption rate observed among the studies of the nonhuman species.

RESULTS

The first step in our analysis involved compiling the estimated predations rates found for 167 cases involving populations of predator-prey pairs wherein both the predator and prey

species were large mammals and for which the individual prey taken were less than a year old (Appendix Table 1 with references shown in Appendix Table 2). The histogram in Figure 1 summarizes these data.

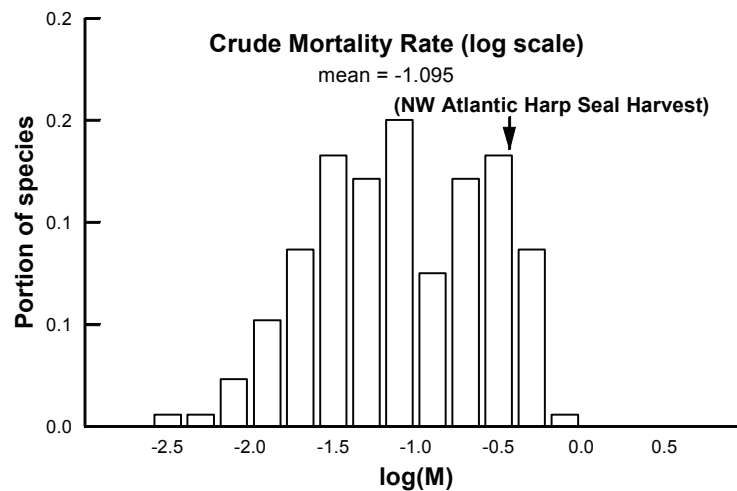


Figure 1.--The harvest of harp seal pups in the northwest Atlantic as it falls in the frequency distribution of predator-specific mortality rates (M) on young-of-the-year for large mammals (from Appendix Table 1).

The harvest of harp seal pups in the northwest Atlantic takes about 37% of the pups (harvest of about 370,000 out of about 1,000,000 born each year, DFO 2000). This harvest ($M = 0.37$) falls within the spectrum of variation in mortality caused by predation among other species as shown in Figure 1 [$\log_{10}(0.37) = -0.43$]. Twenty out of 167 cases of predation exceed this predation rate. The harvest rate (37% per year) is about 4.5-fold larger than the mean of predation rates among nonhuman predators.

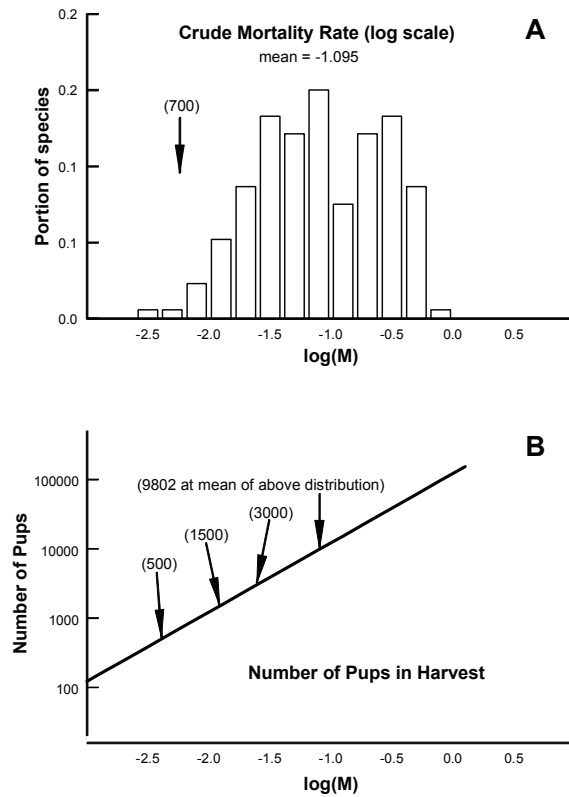


Figure 2.--Frequency distribution of predator-specific mortality rates on young-of-the-year for large mammals (A, from Appendix Table 1) and number of pups that would be taken in a harvest of northern fur seal pups on St. Paul Island, Alaska, as determined by the corresponding mortality rate (B).

Figure 2 presents the data from Figure 1 (Appendix Table 1) along with the estimated mortality rates for a variety of harvests from 500 to 9,802 pups for the northern fur seals on St. Paul Island. Panel A compares a harvest of 700 pups ($M = 700/122,000$) to the variety of consumption rates observed among nonhuman predators. Panel B illustrates the relationship between harvest in numbers and M , both in \log_{10} scale. Thus, the 700 pups from panel A, would

occur on the line just above and to the right of the 500 in panel B. Figure 3(A) shows the same frequency distribution presented in Figures 1 and 2(A) along with the alternative harvest rates for northern fur seal pups on St. George (i.e., $M = 150/17,000$ for the proposed harvest on that island). The maximum harvest shown in this case is 1,390, a value corresponding to the mean consumption rate for nonhuman predators from a population of 17,000.

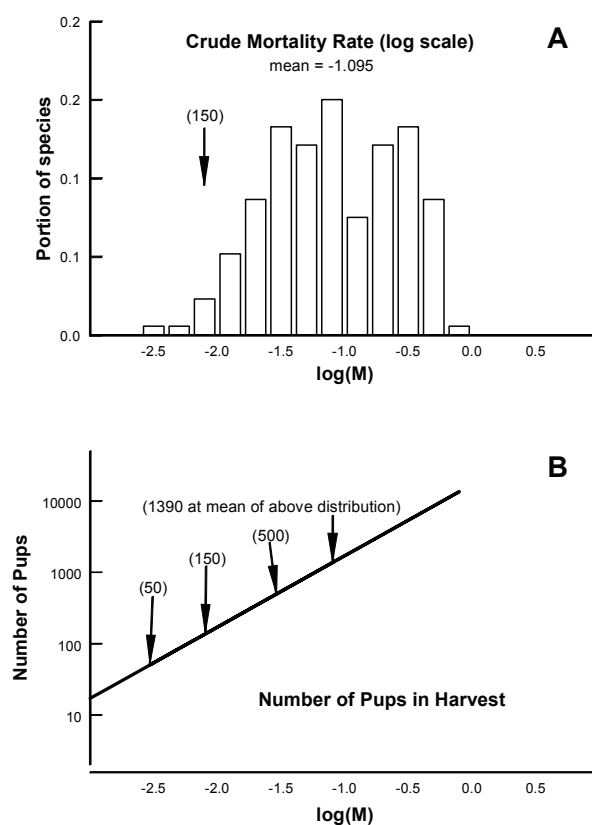


Figure 3.--Frequency distribution of predator-specific mortality rates on young-of-the-year for large mammals (A, from Appendix Table 1) and numbers of pups that would be taken in a harvest of northern fur seal pups on St. George Island, Alaska, as determined by the corresponding mortality rate (B).

Neither the harvest of northern fur seals nor that of harp seal pups lasts a full year. This means that the duration of the season must be accounted for in making comparisons like those shown in Figures 1-3. Short studies, especially those focused on the first few months of life, might easily result in estimated annual mortality rates that are larger than would be the case for studies with a duration of one full year. In other words, short studies conducted just after birth might give rise to biased (elevated) estimates of annual mortality compared to studies lasting all year or from studies conducted late in the first year of life.

The data for the nonhuman species in Figures 1 - 3 are for crude mortality rates estimated for the duration of the study reported in each publication listed in Appendix Table 2 (i.e., some values reported for M are not annual mortality rates). The effect of the length of time over which mortality (often reported as survival which we converted to mortality) was measured and reported in the literature is shown in Figure 4 where our analysis produced inconsistent results. The correlation based on crude rates showed a very slight increase in mortality with the span of time covered by the study (Fig. 4A), as would be expected. In contrast (Fig. 4B), we found that longer studies tended to result in estimated mortality rates that are slightly lower when the analysis is based on a \log_{10} transformation of the data. In view of the small regression coefficients in each case, and the inconsistency, we assumed that the measures we found in the literature could be pooled for comparison (independent of the length of the study). More in-depth analysis of the effects of length of time over which consumption is estimated, and the timing of periods of consumption within the first year of life of the prey are needed.

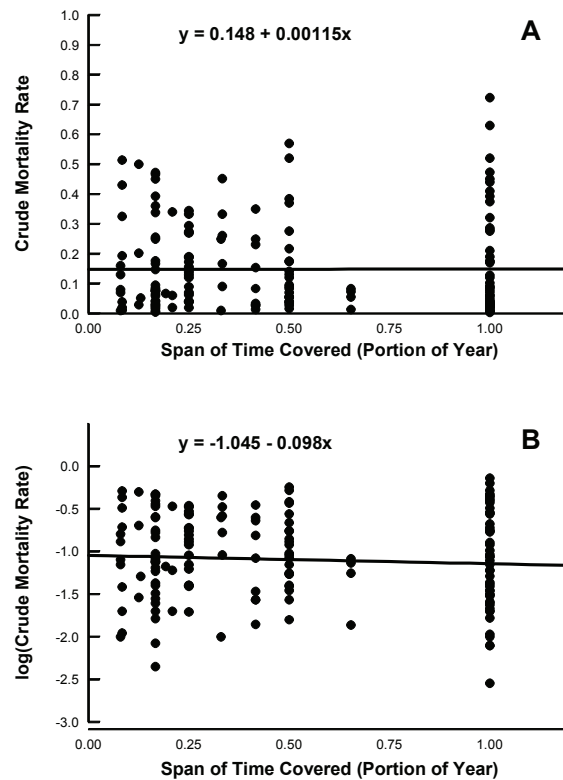


Figure 4.--Estimates of mortality (M = crude mortality rate of Appendix Table 1) as related to span of time covered in the original studies (Appendix Table 2) shown as untransformed values (A) and log-transformed values (B).

Whether or not a harvest is too large is one primary concern (especially from the perspective of concerns about effects on the environment) in regard to the sustainability of our use of natural resources. Such concerns are juxtaposed with the question of whether the harvest is too small, where the importance of sustainability for the consumer is at stake. In the case of northern fur seals (Figs. 2 and 3), the proposed harvest for St. George, and comparable harvests for St. Paul, do not result in mortality rates that are significantly larger than the mortality rates

caused through consumption rates exhibited by nonhuman species. For St. George, 162 of the 167 cases (97%) found in the literature were for predation rates larger than the 0.88% mortality that would be caused by the proposed harvest of 150 pups. Although the comparable harvest (same per capita harvest) rate for St. Paul is slightly different (pup harvest rate of 0.92% per year; $M = 0.0092$) the same number of nonhuman predation rates were larger in the data set in the Appendix (162 out of 167 or about 97%).

Through further analysis of the data in Figure 1 (Appendix Table 1), we explicitly accounted for the number of predators involved. Within the full sample, there was information enabling a count of predators that consumed young-of-the-year in 165 cases. These counts are preliminary, but they contain more information than a hypothetical example; importantly, they help specify the kind of product needed from research to address the management question before us. Figure 5 shows the relationship between predation rates for a particular predator and the total number of predatory species involved in consuming the same prey (i.e., in competition with each other, including the species for which the predation rate is plotted).

As can be seen in the pattern represented in Figure 5, it is likely that there is a decline in predation rates as the number of predators increases – a pattern expected in that the increasing number of predators are sharing finite resources. For example, if there are a total of three competing predatory species, only 4 of the 85 cases (4.7%) represent mortality rates larger than those for the commercial harvest of harp seals (Fig. 6). Thus, the commercial harvest of harp seals is less likely to be sustainable if this species experiences predation by two or more nonhuman mammalian predators, than would be the case if based on the data behind Figure 1,

without direct consideration of predator numbers. For the case of northern fur seals, 5 (5.9%) of the 85 cases where there are three predators are less than the proposed harvest for St. George.

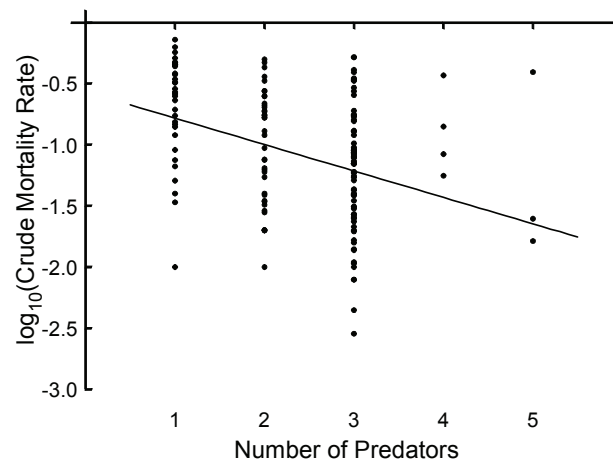


Figure 5.--The pattern of subsets of data from Figure 1 corresponding to the estimated mortality rates as they are observed in correlation with the number of mammalian predators consuming young-of-the-year from each of the respective prey species.

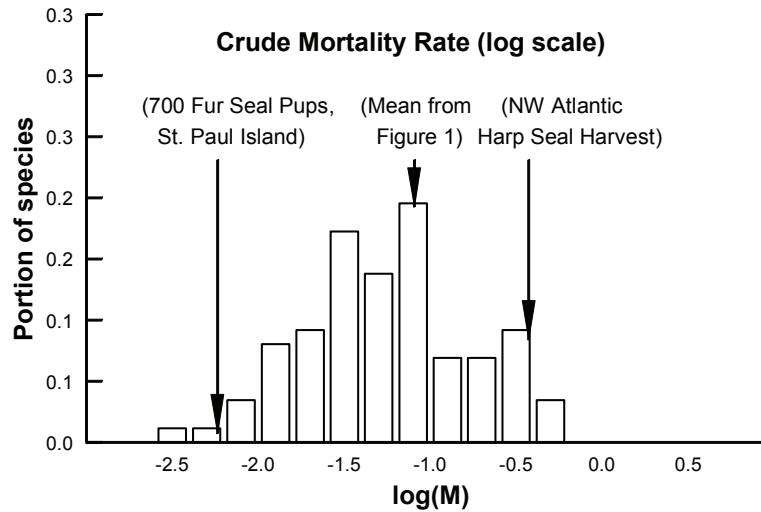


Figure 6. --The subset of data from Figure 1 (see Fig. 5) corresponding to cases where there were three predators involved in the mortality of young-of-the-year (Appendix Table 1), showing the mortality rate from the commercial harvest of harp seals and hypothetical subsistence harvests of northern fur seals (for St. Paul Island) from the Pribilof Islands, Alaska.

The prey of both harp and northern fur seals are species that consume their own prey, each species within its own trophic level. Many of the prey species consumed by both species of seal are not strict herbivores whereas many of the prey in Appendix Table 1 are. Trophic level is another factor behind the question of sustainable harvests and involves one of the ecosystem-based aspects of management. Analyses to treat this factor directly are shown in Figure 7. For these data, there is only one case (one of nine, or 11.1%) where the consumption rates of nonhuman predators exceed the commercial harvest of harp seals. For northern fur seals, there

are no recorded cases where consumption rates by nonhuman predators are less than the proposed harvests on the Pribilof Islands.

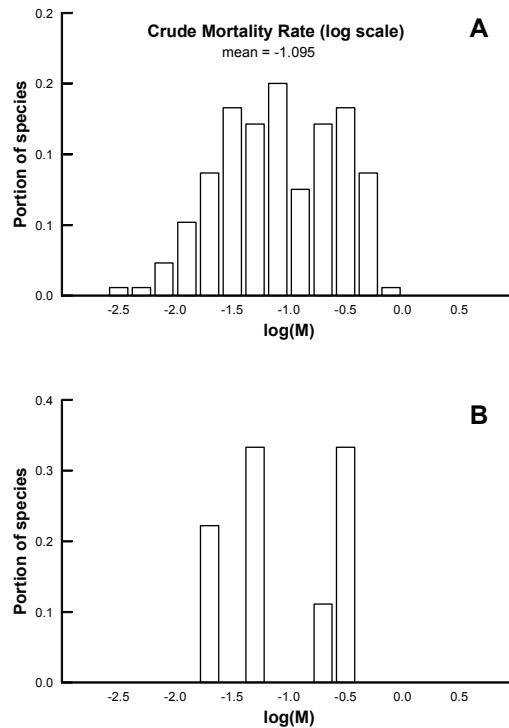


Figure 7.--A comparison of the data from Figure 1 (A) with the subset corresponding to those cases from Appendix Table 1, wherein the predators do not consume herbivores (B, $n = 9$).

DISCUSSION

At the roots of this work is the extremely generic management question: *At what rate can we sustainably harvest?* Harvest is taken from the biosphere, from ecosystems, and from other species (Fowler 2003) and we need to identify the source regarding its hierarchical level (logical

type). Harvest of either harp or northern fur seals is harvest from a specific species (by humans). It is the same as predation on one prey species among nonhuman predatory species – not as measured but as defined (they both fall in the category of consumption of one prey species and both can be measured and compared). Thus, we have the slightly less general management question: *At what rate can we sustainably harvest another species?* The matching (consonant, Belgrano and Fowler 2008) research question is: *At what rates do consumer species consume their prey species?* The empirical pattern consonant with such a general question would have been a plot of predation rates observed for predator-prey pairs as diverse as amoebas consuming bacteria to lions consuming wildebeests or baleen whales consuming krill. Anything beyond the limits of variation observed in such a pattern would be considered an outlier – abnormal and unsustainable regardless of other circumstances or relevant factors (Fowler and Hobbs 2002).

However, the management question behind the specifics of work we are presenting here was much more specific. It involved the human (large mammal) take of young-of-the-year from other large mammal populations. It is known that many elements of ecological systems show patterns related to body size (e.g., Peters 1983, Calder 1984, West et al. 1997, White et al. 2007) and here we are dealing with a situation in which both predator and prey are large mammals. Progressing to further specificity, size is not the only element implied by 'large mammal' – in both cases we are considering mammals. Different taxonomic groups show different behaviors, physiological properties, physiological dynamics, evolutionary histories, population dynamics, and life-history strategies. Much of what large mammals are and do is determined genetically. These factors are to be taken into account in choosing the scientific information used to evaluate proposed action and provide management advice. In this study, we specifically chose

information from the literature regarding large mammal predators taking large mammal prey to match the predator and prey involved in our harvest of seals.

For both harp and northern fur seals, we are dealing with an even more specific management question when harvesting pups: *At what rate can we sustainably harvest young-of-the-year from a large mammal population?* In both cases, we are involved in the take of large mammal prey. In both cases the individuals harvested are younger than 1 year of age. In both cases we want to know if the harvests (or proposed harvests) are sustainable. Thus, the subset of literature that we used in our search was that which contained information from studies of mortality caused by large mammals taking young-of-the-year from their large mammal prey populations, usually reported as the result of studies of prey rather than predators. By doing this, we took into account both size and taxonomy explicitly.

Scientifically, it would be of interest to know how the patterns shown in Figures 1-3, 5 and 7 fit within the overall pattern of predation, from amoebas to whales as predators, and from bacteria to elephants as prey. Factors such as the evolutionary history of the species would be taken into account as inherent to the variation seen in the pattern (Belgrano and Fowler 2008). Correlative patterns (such as that associated with number of predators, Fig. 5 above) within the more general pattern are of great interest. From a practical point of view, they help answer specific questions or concerns exemplified by those raised and addressed above, but addressed here without the benefit of the more general picture/pattern; estimates of consumption rates exist for only a small fraction of the Earth's species.

Revealing the normal in contrast to the abnormal is a crucial role for science in research involving patterns consonant with management questions. It allows for management to avoid the

abnormal – systemic management (Fowler 2003). The matter of observing what is normal compared to what is abnormal can involve either subsets of data specific to the management question (as done in this work) or correlative estimation (that would draw upon more comprehensive sets of data). The latter would involve extrapolation or interpolation from the general pattern whereas the former makes use of a subset of data specific to the management question. Combinations of such approaches would be useful but involves much more research than was possible in the confines of this study.

In this study, we started with a subset of all possible data that matched the generic question to which it applies (*At what rate can we sustainably harvest young-of-the-year from a large mammal population?*). As mentioned earlier, an even more specific sub-set of information would involve predation on young-of-the-year of the precise age at which northern fur or harp seals are taken. Although taken within the first year of life in both cases, the exact ages differ in the case of these two species and different sets of information would be used in each case. The refined management question for northern fur seals would be: *At what rate can we sustainably harvest northern fur seals at 3 to 4 months of age?*, assuming that the harvest would be taken in September and October of each year.

Our choice of data exemplifies the process of ensuring a match (consonance) between management question and guiding information so that the data do not have to be converted in the error prone process of conventional management (Belgrano and Fowler 2008). The management question specifies the units, conditions, and type of information required of the pattern to be found, characterized and displayed through research. The goal is to ensure that the pattern (in reality, data representing the pattern) and question match each other (are consonant or isomorphic

with each other; Fowler and Smith 2004, Belgrano and Fowler 2008). In our case, the first step in achieving a match involved making sure that the units were identical between the pattern and the management question; in each case the units were the portion of the population consumed each year (M). This match was then maintained throughout the process of finding greater specificity in the management question which, early in the process, clearly specified the body size, taxonomic category and age of prey that were involved. In taking this approach, there is no debate or discussion among stakeholders regarding the translation of partially relevant information to the management decision (e.g., body size is partially relevant but not of the units required to answer the management question). The guidance for what to do is inherent to the data chosen; the pattern exposed by research defined by the question provides the answer to the question (i.e., the pattern is in units of M and management avoids abnormal values of M; Fowler and Hobbs 2002).

From our treatment of Figures 1-3, it was clear that we merely initiated the process of refining the management question. Further research would help define the relationship between estimates of M and the length of time covered by a study. However, further or improved research is distinct from the process of refining the management question to direct such research to account for more of the complexity of reality. This process is exemplified above in our consideration of predator numbers and trophic level; the data in hand were analyzed to produce an overt consideration of these factors. Factors such as body size, taxonomic category, age of individuals taken, and the fact we that we were considering predation (as the influence of one species on another) were inherent to the data chosen. As we added further direct consideration of number of predator species and trophic level, we were involved in refinement of the initial

management question, followed, in step, by ensuring a match between the data we used and the refined question. This process continues as further concerns are raised. Stakeholders and scientists are free to contribute to the refinement of the question with their concerns and information. Such concerns are to be translated to refinement of the management question rather than debate about the objective to achieve in management. Following the systemic course, decisions regarding what should be done are based on empirical information rather than debate, political bias, economic factors, or other human values (Belgrano and Fowler 2008). Refinement of the management question further defines the pattern needed for advice (or evaluation). Scientists are led to investigations that have increased focus on more specific patterns and correlative relationships within more general patterns (Fowler 2003).

Most scientists will have little, if any, difficulty understanding that part of the variance observed in the data shown in Figure 1 is explained by research techniques (as scientists we always strive to conduct research according to established standards but cannot be perfect). Other factors contributing to observed variation include the variety of details involved in each specific case (e.g., size of the study area, location, behavioral factors, season, and weather). Few, if any, of the data represent predation rates that apply to the full population of any prey species or the full population of any predatory species. Thus, there is real potential for not only reducing the variance involved in the data representing the real world pattern we most need, but also for finding bias. If it becomes possible to conduct the needed field work, it would be very helpful to explore these factors, both in assuring the quality of science needed to avoid bias and errors of estimation and in assuring consonance with our management questions. With more fully representative data in hand, it would then be possible to deal with the biodiversity of these

systems directly (Fowler 2008). A more comprehensive treatment of the harp seal harvest would almost surely find it to be unsustainable – especially in regard to measures bringing biodiversity into the analysis directly.

We note here that what we have presented above leads to the conclusion that when our interactions with another biological system (e.g., a species) fall within the normal range of natural variation of a generic pattern, it does not guarantee sustainability. Conversely, if they fall outside the normal range of natural variation of such patterns, harvest rates are not sustainable; as outliers, they result in abnormal or unsustainable influence on the nonhuman. For example, the harvest of harp seals at the upper end of the normal range of natural variation seen in Figure 1 may or may not be sustainable in regard to the effects of the harvest on the harp seal species and its ecosystem. The same holds true at the lower end of the spectrum of natural variation. Sustainability is not guaranteed at the lower end of the normal range of natural variation in that the consumption may not be sufficient to sustain the predator population. A harvest of 150 pups would not sustain a population of 100 residents on St. George Island without other sources of food – these kinds of connections and consequences lead to many other management questions.

It is thus obvious that there are many concerns which can be brought to bear in systemic management. Many involve the refinement of management questions. One, for example, involves the number of other prey used by predatory species – a matter of ecological interest. How does this lead to further refinement of our management question? We start with a different scientific question: *How many other sources of food do we humans utilize?* The matching (comparable/consonant) management question is then: *How many species can we sustainably harvest?* We must avoid abnormality in both the harvest of each species and the number of

resource species harvested. Coming back to the matter of harvesting seal pups, this issue leads to a further and quite interesting scientific question: *Are predation rates a function of the number of prey species taken?* This prompts another management question relating to pup harvests: *At what rate can we harvest harp seal pups (or northern fur seal pups) knowing that they are species that consume X species of prey (where X is the count of species in their diet)?*

A very similar concern is that of the number of predators for with the prey serve as a resource (Fig. 5). We are adding ourselves to the list of predators taking northern fur seals and harp seals when we harvest them. This gives rise to the scientific question: *What are the effects of our harvests when we (humans) are one of two, compared to one of five, predators consuming a particular prey species?* We can use the latter issue to illustrate further refinement of the management question central to our consideration of northern fur seals. The management question we began with was: *At what rate can we sustainably harvest young-of-the-year from a large mammal prey base, with Homo sapiens as a large mammal predator?* This specified the science necessary for observing the pattern used for a preliminary evaluation of the proposed harvest of northern fur seal pups on St. George Island (Fig. 3), comparable harvests on St. Paul Island (Fig. 2) and the harvest of harp seals in the northwest Atlantic (Fig. 1).

Moving beyond the initial question, we can now explicitly account for the number of predators involved in the consumption of young-of-the-year (retaining the focus on both the predator and prey as large mammals). This requires refinement of the management question so that it accounts for predator numbers (the numbers of predators feeding on a particular species of prey). Human harvesting contributes to the number of predators involved in the competition for the prey resource by increasing the predator count by one. In the case of both northern fur seals

and harp seals, we are injecting ourselves into a system where the prey are already taken by other predators (regardless of type; e.g., sharks). The new management question becomes: *At what rate can we sustainably harvest young-of-the-year from a large mammal prey base, when, by taking a harvest, the total number of predators (including humans) is N ?* The corresponding research question is: *At what rate are young-of-the-year consumed from a large mammal prey base when the total number of predators is N ?* This was the research question and science behind the production of Figures 5 and 6, confining the predators, in this case, to mammalian predators. A piece of missing information, at this point, is an exact count of the number of mammalian predator species that include northern fur seals (or harp seals) in their diets. Our hypothetical case of three species would include two nonhuman species (e.g., killer whales and Steller sea lions). Adding our predation by harvesting pups on the Pribilof Islands would bring the total to three. The refined management question then becomes: *At what rate can we sustainably harvest young-of-the-year from large mammal populations subject to predation by three mammalian predators?* As exemplified above, research to produce the necessary matching (consonant) pattern, as information for use in management, could focus on the correlative relationship (Fig. 5) between predation rates and numbers of predators that are mammals (without dropping the issues of body size and age of prey).

Continuing to assume that humans bring the total count of mammalian predators to three, another approach involves examining only cases in the literature (or conducting field studies) confined to studies of prey with three species of mammalian predators using them as prey (as shown in Fig. 6). Both approaches continue to support the conclusion that the proposed harvest is of little concern for northern fur seals or their ecosystem (meaning that the proposed

harvest is an acceptably sustainable harvest). In view of the preliminary nature of the data, however, we need more information to better characterize the relationship between numbers of predators and the predation rates on their prey. We are faced with defining research to produce the information needed to guide management or evaluate proposed management action in the case that there is such a relationship. Preliminary information indicates that there is.

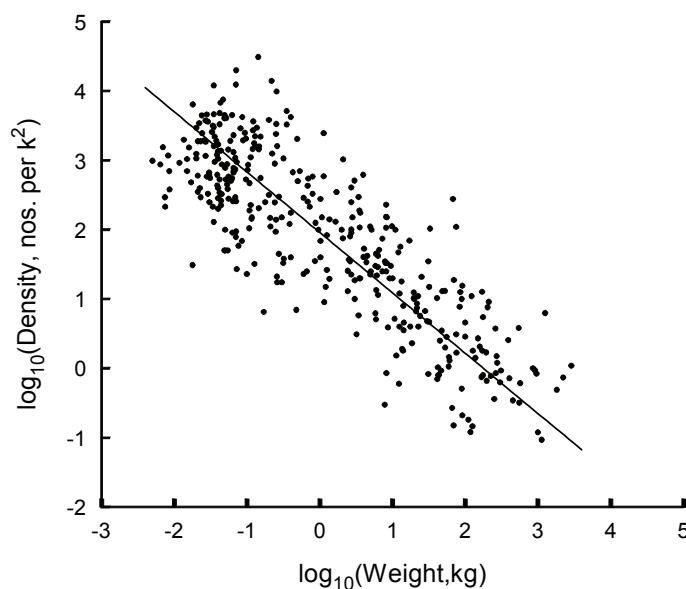


Figure 8.--The empirical pattern in the relationship between population density and body size
(From Damuth 1987).

Another obvious concern involves the status of the prey population. In the case of northern fur seals, the eastern Pacific populations are listed as depleted under terms of the U.S. Marine Mammal Protection Act. We know that, in ecological systems, predator/prey interactions involve what are called functional and numerical responses to population density of prey (an

example of an ecological principle). Predation rates typically drop as the density of prey declines. With this knowledge, we can proceed with further refinement of our management question and further specify the research needed to guide decision-making. The treatment of predator numbers, and trophic level, above involves examples of overt or explicit treatment of general principles inherent to (accounted for by) patterns (Belgrano and Fowler 2008).

Consideration of functional response curves offers the promise of another.

A starting place in this process involves noting a different pattern – that involving a relationship between population density and body size (Fig. 8). Research is needed to determine if this kind of relationship exists for marine species. If such a relationship exists, the relative density of species the size of northern fur seals could be determined from their position relative to the regression line (i.e., a regression line for marine species such as the line for terrestrial species shown in Fig. 8). The predation rates observed for all large mammal prey, including those for terrestrial systems from Appendix Table 1, could then be examined as they relate to the relative density of prey in each case evaluated in relation to the respective regression line. It is conceivable (although only a hypothesis at this point) that a pattern with a mode shifted even farther to the left than that of Figure 5 compared to Figure 1 would emerge for species that are as depleted as northern fur seals are relative to the average population size or density expected for species of their body size. Because the population of northern fur seals remains one of the larger among the various species of marine mammal in the north Pacific (and that of harp seals in the Atlantic), it is also possible that their density is close to the mean expected for species of their body size and the matching pattern would fall more in the central part of the range covered by Figures 1-3.

Questions different from those raised above are also relevant to management – such questions involve different aspects of the management process. The matter of trophic level was treated in Figure 7. There is little evidence that direct consideration of trophic level with a larger sample size would provide grounds for changing our conclusions with regard to either the harvest of harp seals or northern fur seals; in other words, panel B of Figure 7 appears to show little if any difference from a random sample of cases from panel A. Further research to test this hypothesis and to provide a larger sample size would clearly be useful.

Another issue of concern involves population trends. For example, the population of northern fur seals has been declining over the past 20 years (Towell et al. 2006). If it continues, the question arises: *When would a harvest of 150 pups on St. George become unsustainable?* The pattern in consumption rates among nonhuman predators as they relate to population status of their prey would be used to determine such sustainability – following the approach outlined above for population status in general. For example, the population of northern fur seals on St. George would have to drop to a level where only 1,867 pups were born in the population each year in order for a harvest of 150 to correspond to the mean mortality rate observed in the data from Appendix Table 1. This is approximately 10% of the current population. This example, however, fails to account explicitly for functional responses (discussed above), numbers of predators (e.g., Fig. 5), and other elements of complexity, more of which are outlined below in showing how such factors can be accounted for in refined management questions.

Also of concern in managing our harvest of resources is the issue of the location or distribution of harvests in geographic space. On the Pribilof Islands, this is a matter of asking a number of different management questions. Assuming that we are still specifically treating

harvests of young-of-the-year of northern fur seals, one such question would be: *What portion of the island-wide harvest should be taken from each rookery area?* To make this question specific to St. George (the same can be done for St. Paul), it would be: *What portion of the island-wide harvest on St. George should be taken from each rookery area?* A simple answer to this question might be found by assuming that nonhuman predators consume pups from the rookeries in proportion to the number of pups born on each rookery. This being the case, we can assume that pup numbers are distributed in proportion to the number of adult male northern fur seals that hold territories with females in their territories for each rookery (these are counted each year). Under these assumptions, 14 of the 150 pups proposed to be harvested on St. George would be taken from Zapadni rookery, 32 from South, 54 from North, 12 from East Reef, 30 from East Cliffs, and 8 from Staraya. If studies were to show a different distribution of harvest rates among nonhuman predators, the pattern observed could be used to allocate the harvest in a similar distribution. If there is variation among predators in their allocation of predation among the various rookeries, this would be used to conclude that similar variation is an option for the subsistence harvest.

A different approach would be to assess the question: *Is the proposed harvest of 150 pups on St. George Island sustainable if taken from any one rookery area?* Figure 9 shows the resulting rookery-specific mortality rates in comparison to observed mortality among nonhuman predators, again assuming that pup numbers are distributed among rookeries in proportion to the distribution of adult territorial male with females in their territories. In other words, Figure 9 shows the mortality rates that would result from taking all 150 pups from each one (but only one) of the six rookery areas, with one mortality rate for each rookery area (each rookery area is

identified by its corresponding letter above the arrow depicting the mortality rate for that rookery area). Thus, in Figure 9, these mortality rates are again compared to the mortality rates listed in Appendix Table 1 and shown in earlier evaluations of the island-wide mortality rates.

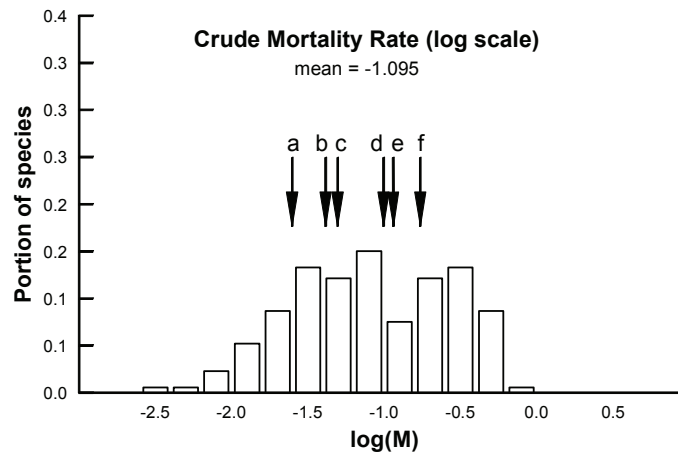


Figure 9.--The rookery-specific mortality rates for St. George Island, assuming that the harvest would be 150 northern fur seal pups in each case, in comparison to predator-specific mortality rates on young-of-the-year for large mammals shown in a frequency distribution of the data from Appendix Table 1. The individual rookeries are (letters corresponding to arrows depicting the associated mortality rates): a: North, b: South, c: East Cliffs, d: Zapadni, e: East Reef, f: Staraya.

The results of this comparison show that each rookery-specific case of mortality caused by a harvest of 150 pups falls within the normal range of natural variation observed among nonhuman large-mammal predators in their take of young-of-the-year from other large mammal populations. In all cases, of course, the mortality rate is larger than would be the case if the

harvest were spread evenly among all rookeries (Fig. 3). However, if taken from only one rookery, it is also clear that the harvest should be taken from North rookery, the largest rookery on the island (arrow a, the smallest mortality rate in Fig. 9). This would amount to choosing a rookery where the impact would be most sustainable (in terms of minimizing effects on the population and ecosystem). The distribution of harvests within a rookery are of similar concern and should also be dealt with to avoid abnormality.

The examples we have presented and discussed above serve to illustrate the process of asking questions, refining questions, and conducting research to obtain the match needed among the questions and patterns that serve as guiding information. As indicated above, this match involves identical units of measure, identical logical type, and isomorphism, or what is known as consonance (Fowler and Smith 2004, Belgrano and Fowler 2008). Further progress would be seen in research looking for patterns in predation rates related to latitude and the extent of overlap in the geographic ranges of predator and prey. In the cases of humans harvesting marine mammals, we would want to know if there are correlative patterns within the information from Appendix Table 1 related to cases where terrestrial species are predators on marine mammals species.

Many such questions can be asked regarding issues related to birth rates, environmental conditions, life history and reproductive strategy. As research questions, these include: *Are there patterns in which the predation rates on prey species that give birth primarily to twins different from those that give birth to single offspring? Are there patterns in which predation rates differ between years of El Niño events and non-El Niño events? Are there patterns in the predation rates of prey when they are highly migratory species (such as the northern fur seal)?* The timing

of the short studies within the first year of life also undoubtedly contributes to the variance observed in the overall pattern, in spite of the lack of evidence for such a pattern in this study. In view of the survivorship/age relationship seen in most species (and specifically northern fur seals, Barlow and Boveng 1991), we would expect a relationship (pattern) observed in a correlation between mortality rate and age, specific to the weeks and months within the first year of life. *What is that relationship?* These are scientific questions important in refining the management question; the management question specifies the combination of such factors which, in turn, determines the pattern to be produced by research that matches the management question.

Thus, a few of the factors listed in the preceding paragraphs can be used to generate a management question reflecting a bit more of the complexity of the situation faced in the harvest of young-of-the-year from harp and northern fur seals. The complexity behind such factors is endless as would be a complete list of such factors. However, we can think of a few such factors and our best efforts would be brought to bear in making the list as extensive as possible. An example for northern fur seals (assuming a harvest in October) would be initiated with: *At what rate can we sustainably harvest*

- *young-of-the-year*
- *taken in the fourth month of life*
- *for a highly migratory*
- *pinniped (inferred to be a large mammal)*
- *in the Bering Sea (thus including marine compared to terrestrial)*
- *with a population less than 50% of its historically observed peak*
- *during years of non-El Niño events,*

- and already subject to predation by 6 species of predators

- for a predator that is a terrestrial large mammal?

If the related analyses of variance of data such as those shown in Figure 1 show sub-patterns or correlations with the identified factors (as was demonstrated in Figs. 5 and 6), these patterns can be used to demonstrate the normal (sustainable) and abnormal (unsustainable), with much more clarity regarding what is unsustainable to account for the circumstances involved in each of the three cases we are treating.

Things are too complex to be able to assume that the job of management is finished by addressing and implementing management regarding any one of the individual management issues listed above. Even the questions above fail to explicitly address all the aspects of management (complexity) involved. To account for complexity as best we can, we need to formulate as many questions as possible – bringing into the question-asking phase of management the concerns of all stakeholders. As such concerns are raised, the related issues must be addressed through either refined management questions, or distinctly different management questions. Refined management questions were exemplified in cases such that behind Figs. 5 - 7 above. A distinctly new management question was exemplified above, when we raised the issue of distribution of harvests (keeping in mind that management questions are, in reality, all interrelated). It was a question distinct from the questions related to harvest rates.

Another distinct question stems from knowledge that ecological systems vary. Is it realistic to implement management based on a specific fixed number for harvests? The proposed harvest of 150 pups on St. George could over-simplistically result in policy requiring that exactly 150 pups (no more and no less) be taken each year. Or, a take of no more than 150 pups might be

written into regulations. Is this realistic? We saw that continued reduction in the northern fur seal population could result in reduced harvests – one form of change, or temporal variation. What about the situation where little else is known to be changing? We are brought to the management question: *How much year-to-year variation should there be in the harvest of northern fur seal pups from St. George Island?*

This question can be addressed in parallel with other questions as raised above, but would require its own set of question-specific data. Science would again focus on description and analysis of a pattern that matches the management question. In this specific case, research to provide the guidance would involve studies to determine the variance in year-to-year predation rates among nonhuman predators in their consumption of young-of-the-year. Most useful here would be data on the coefficient of variation so that the issue of the magnitude of the rates themselves can be left to be treated with data such as those presented above. To then be realistically applied, management would require that there be year-to-year variation in the harvest to mimic variation seen in empirical data from real-world cases observed for nonhuman predator-prey systems. As with the other examples above, the matters of body size, extenuating circumstances, trophic level, and other factors would be used to refine the question and provide more quantitative substance to the intraspecific patterns that match the question. *A priori*, it is clear that it would be unrealistic to implement management that would confine the harvest to a fixed level – no other predator species consumes its prey at a fixed rate.

As noted repeatedly, and specifically in the last paragraph, extenuating circumstances cannot be ignored in management. A major factor to acknowledge in today's world is that of human influence on our environment. The systems from which data are collected and the

systems about which we are asking the management question are all influenced by factors such as pollution, global warming, harvests of other species the list is essentially endless, especially in view of the many indirect effects of such factors. The extent and nature of the effects of many such influential factors are nearly impossible, if not impossible, to clearly establish in a convincing scientific manner. One of the major advantages of using natural patterns as a basis for decision-making is that they integrate (include being a product of, so as to reflect) the effects of human influence (Belgrano and Fowler 2008), and specifically the effects listed above. Thus, the position and nature of patterns such as those shown in Figure 1 (including any trends or changes involved), automatically account for the collective effects of such human ‘disturbance’ whether it be of global warming, pollution, past harvests of cetacean species, or oceanic acidification.

Knowing that such factors contribute to variance and its limitations, however, fails to provide specificity with respect to management questions and informative patterns. An overt/explicit accounting for such factors is possible in two ways. First, they can be addressed with different or distinct management questions (*At what rate can we sustainably produce CO₂? At what rate can we sustainably produce pesticides? At what rate can we sustainably consume other resource species?* – see Fowler and Hobbs 2002, and Fowler 2008 for examples of patterns to be used in addressing such questions). Second, they can be addressed in correlative/sub-pattern analysis to refine the management question. In this case, a set of elements would be added to the list above; for example,

- under conditions of current global temperature regimes,
- with pollution levels currently observed, and

- when other species are subjected to existing harvests by humans.

Such a list can be extended indefinitely. If none of the observed predation rates (spatial allocations or variance in predation rates) among nonhuman species can be found to show a correlation with any of these factors, we are left with the confidence that they are already accounted for in the data, implicitly – data that can be used to account for other known correlative patterns, explicitly (keeping mind, always, the inherent quality of the data and the quality of the research that produces them). The precautionary reversal of the burden of proof (Peterman 1990, Gerrodette et al. 2002) is inherent to this process.

Another factor of concern involves the genetic effects of harvesting. The proposed harvest of northern fur seal pups from the St. George community is for 150 males; males would be selected in preference to females and the harvest would be of only (or primarily) one sex. The proposed selectivity can easily be understood, based on the fact(s) that there was a commercial harvest of subadult males that lasted decades without discernable negative effects on the population. Population models show that a harvest of males has a much smaller effect on production than does either a harvest of both sexes selected randomly, or a harvest of only females (Fowler et al. 1980). Northern fur seals are a species with an extreme polygynous breeding system (Gentry and Kooyman 1986); higher natural mortality is observed among males than females (and, therefore, there is a highly skewed sex ratio), and nearly all species depend on females for reproduction more than they depend on males. In view of these isolated facts, a male harvest seems to make sense. The situation is much more complicated than this, however, and management needs to be consistent in its various applications and particularly needs to be evolutionarily enlightened (Thompson 2005) by accounting for selectivity (Etnier and Fowler

2005). If we are to meet these demands, especially to account for the effects of selectivity, the sex-composition of the harvest would match the sex-composition of the seals taken in the consumption by predators. This is probably quite close to the sex composition of the 0-1 year-old age class in the population. If the focus on males is approved as a management decision, it must be recognized as an example of conventional management rather than systemic management. As conventional management, it would be application of what Belgrano and Fowler (2008) call misdirected reductionism, subject to the consequences of abnormal selectivity, and would only partially account for the complexity of factors that need to be brought to bear in decision-making. The same concerns apply to size: selective harvesting of large healthy pups could easily have a genetic effect that is quite abnormal compared to that of the nonhuman predators.

Conventional approaches to evaluating the harvest of pups would entail a variety of options one of which might be an analysis in which a simulation model of the population would be used to make predictions of population decline that can be attributed to the harvest. In conventional thinking, this option is emphasized in the case of northern fur seals because of the observed decline and depleted status of the population of this species. Such an approach invites the judgment of experts or other stakeholders. This introduces bias and error. A team of managers and scientists, for example, would translate the information regarding projected decline to a management decision – a harvest restriction. This conversion is an example of how current management inherently involves human error, bias, limitations, and values. The conversion is essentially guesswork. This happens, for example, if it were to be shown that a harvest of 150 pups on St. George Island leads to a population 3% less than otherwise expected after 25 years.

The decline, a measure of temporal change in expected population level, would be converted to predation rates – they are two different things and cannot be converted in the debate of a decision-making process. In other words, temporal population change would be converted to predation rates in an artificial process; the resulting subsistence harvest would be a result of the management decision based on consideration of the population decline out of context – an illogical connection. The units or dimensions of the management (those specified by the management question – predation rates) would not match the information being used (difference in projected population level). Concern about that effect (the difference in projected population level) would result in restrictions on the harvest that would replace action taken to correct other anthropogenic abnormalities in the northern fur seal's ecosystem which would go uncorrected. In systemic management the other abnormalities would be dealt with systematically on a case by case basis. Mitigating action to deal with those factors places the burden on other elements of the overall system. In this case, denying the people of the Pribilof Islands their request to harvest northern fur seals is a form of mitigation that avoids dealing directly with other problems clearly measurable as human abnormality.

SUMMARY

Data for 167 cases of predation by nonhuman predators on large mammal prey less than 1 year old were used to evaluate the harp seal harvest in the northwest Atlantic and a proposed harvest of 150 northern fur seal pups on St. George Island, Alaska. A similar potential harvest of 1,125 pups on St. Paul Island (same number of pups per island resident with an assumed human population of 750) was also evaluated. The harp seal harvest is exceeded by only 20 (about 12%)

of the 167 cases with no further analysis of the overall pattern. This rate may be unsustainable if other factors are taken into account – specifically factors such as numbers of predators involved and the trophic levels of these species. Only 4.7% of the cases where there are three predators (4 of the 85 of the original 167) have estimated predation rates larger than that of the commercial harvest of harp seal pups in the northwest Atlantic. Other factors to consider overtly include the number of alternative prey predators consume, and the fact that humans are a terrestrial predator preying on marine prey (which would lead to comparisons involving nonhuman terrestrial predators feeding on marine mammal young-of-the-year). Further research is needed, but the harp seal harvest is probably not sustainable (i.e., is probably abnormal compared to other species when the complexity of the system is accounted for directly).

For northern fur seals, the overall pattern among nonhuman large mammal species (for both predator and prey) provides no scientific basis for rejecting the proposed harvest of 150 pups on St. George Island, Alaska (or a comparable harvest of 1,125 on St. Paul, Island). This conclusion is based on evaluations using the pattern among nonhuman species as an integrative pattern to account for the complexity of the full suite of factors involved in natural systems (including ecosystems and the biosphere; Fowler 2003, Belgrano and Fowler 2008). Concerns about a declining northern fur seal population emphasize the need to focus overtly, or explicitly, on a variety of these factors (in addition to body size, taxonomic category, and age already accounted for explicitly). As mentioned above, there is need to deal overtly with patterns in functional response dynamics to ensure that we avoid abnormal harvest rates in accounting for the decline in northern fur seals. But there is also a very important need to examine patterns regarding the sustainability of the numerous other human activities and influences that directly or

indirectly are related to both the pattern we used and the decline of northern fur seals through the interconnected nature of ecosystems and the biosphere. These factors include fisheries harvests, pollution, and CO₂ production (related to oceanic acidification and global warming).

Management to relieve systems of abnormal human influence based on patterns related to such issues would replace complete prohibition of the harvest of pups. Harvesting pups obviously will contribute to declining trends but management action to prohibit such harvests would be carried out only if the harvest rates themselves are found to be abnormal for existing circumstances. Because nonhuman predators would terminate their consumption of their prey species when the prey population reaches certain low threshold levels (with a minimum of zero), the harvest would be prohibited under similar circumstances.

In the case of proposed northern fur seal harvests (for both Pribilof islands), the resulting predation rates under existing circumstances would be well below the bulk of predation rates observed for nonhuman species, regardless of circumstances that we have examined. Further refinement of the management question, could lead to the conclusion that a larger portion of nonhuman predation rates are larger than such harvests would represent, but the harvest rates are small enough to fall in the lower end of the frequency distribution of most subsets of data for other large mammals. This means that the proposed annual harvest of 150 pups on St. George Island (and comparable harvests on St. Paul Island) can be considered sustainable for the foreseeable future. Continued monitoring and research, especially of the kind exemplified in this paper, is needed.

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APPENDICES

Appendix Table 1 lists prey species and their predatory species for which the references in Appendix Table 2 served as sources of estimated mortality rates on young-of-the-year for the prey population as caused by the population of each specific predator. Also included in Appendix Table 1 are counts of the large mammal predators known to be predators on the prey populations as reported in the studies listed in Appendix Table 2.

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Appendix Table 1.--List of prey for which young-of-year mortality rates caused by specific predators were found in the literature as identified by the reference number (found in the literature cited section as identified in Table 2).

Prey	Predator	Citation Number	Mortality Rate (M)	Number of Predators
<i>Acinonyx jubatus</i>	<i>Crocutta crocutta</i>	50	0.025	5
<i>Acinonyx jubatus</i>	<i>Panthera leo</i>	50	0.393	5
<i>Alces alces</i>	<i>Canis lupus</i>	7	0.060	3
<i>Alces alces</i>	<i>Canis lupus</i>	16	0.175	3
<i>Alces alces</i>	<i>Canis lupus</i>	45	0.147	1

Appendix Table 1.--Cont.

<i>Alces alces</i>	<i>Canis lupus</i>	45	0.194	1
<i>Alces alces</i>	<i>Canis lupus</i>	48	0.120	3
<i>Alces alces</i>	<i>Canis lupus</i>	49	0.041	
<i>Alces alces</i>	<i>Canis lupus</i>	55	0.070	3
<i>Alces alces</i>	unidentified predator	7	0.020	3
<i>Alces alces</i>	unidentified predator	16	0.025	3
<i>Alces alces</i>	<i>Ursus americanus</i>	7	0.340	3
<i>Alces alces</i>	<i>Ursus americanus</i>	16	0.035	3
<i>Alces alces</i>	<i>Ursus americanus</i>	48	0.030	3
<i>Alces alces</i>	<i>Ursus americanus</i>	55	0.090	3
<i>Alces alces</i>	<i>Ursus americanus</i>	57	0.091	1
<i>Alces alces</i>	<i>Ursus americanus</i>	62	0.034	1
<i>Alces alces</i>	<i>Ursus arctos</i>	7	0.060	3
<i>Alces alces</i>	<i>Ursus arctos</i>	16	0.410	3
<i>Alces alces</i>	<i>Ursus arctos</i>	48	0.520	3
<i>Alces alces</i>	<i>Ursus arctos</i>	55	0.520	3
<i>Alces alces andersoni</i>	<i>Ursus americanus</i>	66	0.440	1
<i>Alces alces gigas</i>	<i>Canis lupus</i>	6	0.020	2
<i>Alces alces gigas</i>	<i>Canis lupus</i>	18	0.014	3
<i>Alces alces gigas</i>	<i>Canis lupus</i>	22	0.020	3
<i>Alces alces gigas</i>	unidentified bear	18	0.027	3
<i>Alces alces gigas</i>	unidentified predator	6	0.020	2

Appendix Table 1.--Cont.

<i>Alces alces gigas</i>	unidentified predator	18	0.027	3
<i>Alces alces gigas</i>	unidentified predator	22	0.039	3
<i>Alces alces gigas</i>	<i>Ursus americanus</i>	18	0.350	3
<i>Alces alces gigas</i>	<i>Ursus americanus</i>	22	0.333	3
<i>Alces alces gigas</i>	<i>Ursus arctos</i>	6	0.430	2
<i>Alces alces gigas</i>	<i>Ursus arctos</i>	18	0.027	3
<i>Alces alces gigas</i>	<i>Ursus arctos</i>	22	0.294	3
<i>Alces gigas</i>	<i>Canis lupus</i>	25	0.092	3
<i>Alces gigas</i>	<i>Canis lupus</i>	26	0.630	1
<i>Alces gigas</i>	unidentified predator	25	0.078	3
<i>Alces gigas</i>	<i>Ursus americanus</i>	25	0.393	3
<i>Alces gigas</i>	<i>Ursus arctos</i>	25	0.031	3
<i>Antilocapra americana</i>	<i>Aquila chrysaetos</i>	3	0.010	2
<i>Antilocapra americana</i>	<i>Aquila chrysaetos</i>	35	0.029	2
<i>Antilocapra americana</i>	<i>Canis latrans</i>	3	0.010	1
<i>Antilocapra americana</i>	<i>Canis latrans</i>	32	0.339	3
<i>Antilocapra americana</i>	<i>Canis latrans</i>	35	0.500	2
<i>Antilocapra americana</i>	<i>Canis latrans</i>	61	0.333	2
<i>Antilocapra americana</i>	<i>Lynx rufus</i>	3	0.250	2
<i>Antilocapra americana</i>	<i>Lynx rufus</i>	32	0.032	2
<i>Antilocapra americana</i>	<i>Lynx rufus</i>	61	0.167	2
<i>Antilocapra americana</i>	unidentified predator	32	0.065	2

Appendix Table 1.--Cont.

<i>Antilocapra americana</i>	unidentified predator	35	0.202	2
<i>Arctocephalus australis</i>	<i>Otaria byronia</i>	19	0.067	1
<i>Arctocephalus gazella</i>	<i>Hydrurga leptonyx</i>	10	0.344	1
<i>Arctocephalus pusillus pusillus</i>	<i>Canis mesomelas</i>	9	0.375	1
<i>Callorhinus ursinus</i>	<i>Eumetopias jubatus</i>	28	0.051	1
<i>Capreolus capreolus</i>	<i>Canis familiaris</i>	49	0.011	3
<i>Capreolus capreolus</i>	<i>Canis lupus</i>	49	0.021	3
<i>Capreolus capreolus</i>	<i>Lynx lynx</i>	49	0.031	3
<i>Capreolus capreolus</i>	<i>Vulpes vulpes</i>	36	0.467	1
<i>Capreolus capreolus</i>	<i>Vulpes vulpes</i>	40	0.450	1
<i>Cervus canadensis</i>	<i>Puma concolor</i>	8	0.140	1
<i>Cervus canadensis</i>	<i>Puma concolor</i>	59	0.094	2
<i>Cervus canadensis</i>	unidentified predator	59	0.075	2
<i>Cervus canadensis</i>	<i>Ursus americanus</i>	59	0.472	2
<i>Cervus elaphus</i>	<i>Aquila chrysaetos</i>	15	0.008	3
<i>Cervus elaphus</i>	<i>Canis familiaris</i>	49	0.003	3
<i>Cervus elaphus</i>	<i>Canis latrans</i>	13	0.028	2
<i>Cervus elaphus</i>	<i>Canis latrans</i>	15	0.087	3
<i>Cervus elaphus</i>	<i>Canis lupus</i>	49	0.070	3
<i>Cervus elaphus</i>	<i>Lynx lynx</i>	49	0.017	3
<i>Cervus elaphus</i>	unidentified bear	15	0.024	3
<i>Cervus elaphus</i>	unidentified predator	15	0.008	3

Appendix Table 1.--Cont.

<i>Cervus elaphus</i>	<i>Ursus americanus</i>	13	0.076	2
<i>Cervus elaphus</i>	<i>Ursus americanus</i>	15	0.008	3
<i>Cervus elaphus</i>	<i>Ursus arctos</i>	15	0.087	3
<i>Equus caballus</i>	<i>Puma concolor</i>	47	0.173	1
<i>Equus caballus</i>	<i>Puma concolor</i>	52	0.451	1
<i>Lama guanicoe</i>	<i>Puma concolor</i>	46	0.473	1
<i>Odocoileus hemionus</i>	<i>Aquila chrysaetos</i>	67	0.083	
<i>Odocoileus hemionus</i>	<i>Canis latrans</i>	1	0.276	2
<i>Odocoileus hemionus</i>	<i>Canis latrans</i>	21	0.120	2
<i>Odocoileus hemionus</i>	<i>Canis latrans</i>	29	0.270	1
<i>Odocoileus hemionus</i>	<i>Canis latrans</i>	33	0.385	1
<i>Odocoileus hemionus</i>	<i>Canis latrans</i>	34	0.130	3
<i>Odocoileus hemionus</i>	<i>Canis latrans</i>	38	0.723	1
<i>Odocoileus hemionus</i>	<i>Canis latrans</i>	44	0.325	1
<i>Odocoileus hemionus</i>	<i>Canis latrans</i>	67	0.250	1
<i>Odocoileus hemionus</i>	feline (<i>Lynx rufus</i> or <i>Puma concolor</i>)	34	0.039	3
<i>Odocoileus hemionus</i>	<i>Lynx rufus</i>	1	0.035	2
<i>Odocoileus hemionus</i>	mostly <i>Canis latrans</i>	14	0.570	1
<i>Odocoileus hemionus</i>	mostly <i>Canis latrans</i>	14	0.120	1
<i>Odocoileus hemionus</i>	<i>Puma concolor</i>	8	0.040	1
<i>Odocoileus hemionus</i>	<i>Puma concolor</i>	21	0.130	2

Appendix Table 1.--Cont.

<i>Odocoileus hemionus</i>	unidentified predator	21	0.190	2
<i>Odocoileus hemionus</i>	<i>Ursus americanus</i>	34	0.039	3
<i>Odocoileus hemionus</i>	<i>Canis latrans</i> or <i>Ursus</i>	64	0.063	2
<i>columbianus</i>	<i>americanus</i>			
<i>Odocoileus hemionus</i>	<i>Puma concolor</i>	64	0.188	2
<i>columbianus</i>				
<i>Odocoileus hemionus crookii</i>	<i>Canis latrans</i>	60	0.231	1
<i>Odocoileus hemionus crookii</i>	unidentified predator	60	0.154	1
<i>Odocoileus virginianus</i>	<i>Canis familiaris</i>	24	0.055	2
<i>Odocoileus virginianus</i>	<i>Canis familiaris</i>	30	0.084	4
<i>Odocoileus virginianus</i>	<i>Canis familiaris</i>	31	0.016	3
<i>Odocoileus virginianus</i>	<i>Canis familiaris</i>	42	0.020	2
<i>Odocoileus virginianus</i>	<i>Canis familiaris</i>	51	0.027	3
<i>Odocoileus virginianus</i>	<i>Canis familiaris</i>	53	0.034	2
<i>Odocoileus virginianus</i>	<i>Canis familiaris</i>	63	0.020	2
<i>Odocoileus virginianus</i>	<i>Canis latrans</i>	4	0.250	2
<i>Odocoileus virginianus</i>	<i>Canis latrans</i>	4	0.167	2
<i>Odocoileus virginianus</i>	<i>Canis latrans</i>	5	0.360	2
<i>Odocoileus virginianus</i>	<i>Canis latrans</i>	24	0.040	2
<i>Odocoileus virginianus</i>	<i>Canis latrans</i>	30	0.370	4
<i>Odocoileus virginianus</i>	<i>Canis latrans</i>	38	0.321	1
<i>Odocoileus virginianus</i>	<i>Canis latrans</i>	39	0.217	2

Appendix Table 1.--Cont.

<i>Odocoileus virginianus</i>	<i>Canis latrans</i>	43	0.083	3
<i>Odocoileus virginianus</i>	<i>Canis latrans</i>	44	0.514	1
<i>Odocoileus virginianus</i>	<i>Canis latrans</i>	51	0.054	3
<i>Odocoileus virginianus</i>	<i>Canis latrans</i>	53	0.276	2
<i>Odocoileus virginianus</i>	<i>Canis latrans</i>	58	0.059	3
<i>Odocoileus virginianus</i>	<i>Canis lupus</i>	42	0.039	2
<i>Odocoileus virginianus</i>	<i>Canis lupus</i>	63	0.210	2
<i>Odocoileus virginianus</i>	<i>Lynx rufus</i>	4	0.075	1
<i>Odocoileus virginianus</i>	<i>Lynx rufus</i>	5	0.020	2
<i>Odocoileus virginianus</i>	<i>Lynx rufus</i>	30	0.056	4
<i>Odocoileus virginianus</i>	<i>Lynx rufus</i>	31	0.095	3
<i>Odocoileus virginianus</i>	<i>Lynx rufus</i>	43	0.014	3
<i>Odocoileus virginianus</i>	<i>Lynx rufus</i>	51	0.027	3
<i>Odocoileus virginianus</i>	<i>Lynx rufus</i>	56	0.255	3
<i>Odocoileus virginianus</i>	<i>unidentified predator</i>	31	0.175	2
<i>Odocoileus virginianus</i>	<i>unidentified predator</i>	43	0.056	3
<i>Odocoileus virginianus</i>	<i>unidentified predator</i>	51	0.027	3
<i>Odocoileus virginianus</i>	<i>unidentified predator</i>	53	0.034	2
<i>Odocoileus virginianus</i>	<i>unidentified predator</i>	58	0.059	3
<i>Odocoileus virginianus</i>	<i>Ursus americanus</i>	30	0.141	4
<i>Odocoileus virginianus</i>	<i>Ursus americanus</i>	39	0.174	2
<i>Odocoileus virginianus</i>	<i>Ursus americanus</i>	43	0.073	3

Appendix Table 1.--Cont.

<i>Odocoileus virginianus</i>	<i>Ursus americanus</i>	58	0.176	3
<i>Odocoileus virginianus</i>	<i>Vulpes</i> or <i>Urocyon</i> spp.	31	0.016	3
<i>Odocoileus virginianus</i>	<i>Vulpes vulpes</i> or <i>Urocyon</i> <i>cinereoargenteus</i>	56	0.085	3
<i>Oreamnos americanus</i>	<i>Canis latrans</i>	41	0.103	3
<i>Oreamnos americanus</i>	<i>Puma concolor</i>	41	0.051	3
<i>Oreamnos americanus</i>	unidentified predator	41	0.026	3
<i>Oreamnos americanus</i>	<i>Ursus americanus</i>	41	0.128	3
<i>Ovis canadensis</i>	<i>Puma concolor</i> or <i>Canis</i> <i>latrans</i>	37	0.452	1
<i>Phoca hispida</i>	<i>Alopex lagopus</i>	20	0.261	1
<i>Phoca hispida</i>	<i>Ursus maritimus</i>	12	0.287	1
<i>Rangifer tarandus</i>	<i>Aquila chrysaetos</i>	2	0.038	3
<i>Rangifer tarandus</i>	<i>Aquila chrysaetos</i>	17	0.070	3
<i>Rangifer tarandus</i>	<i>Aquila chrysaetos</i>	23	0.080	3
<i>Rangifer tarandus</i>	<i>Aquila chrysaetos</i>	23	0.010	3
<i>Rangifer tarandus</i>	<i>Canis latrans</i>	17	0.040	3
<i>Rangifer tarandus</i>	<i>Canis lupus</i>	2	0.011	3
<i>Rangifer tarandus</i>	<i>Canis lupus</i>	17	0.274	3
<i>Rangifer tarandus</i>	<i>Canis lupus</i>	23	0.160	3
<i>Rangifer tarandus</i>	<i>Canis lupus</i>	23	0.170	3
<i>Rangifer tarandus</i>	<i>Gulo gulo</i>	23	0.010	3

Appendix Table 1.--Cont.

<i>Rangifer tarandus</i>	<i>Lynx canadensis</i>	54	0.080	3
<i>Rangifer tarandus</i>	<i>unidentified predator</i>	17	0.090	3
<i>Rangifer tarandus</i>	<i>unidentified predator</i>	23	0.070	3
<i>Rangifer tarandus</i>	<i>unidentified predator</i>	23	0.060	3
<i>Rangifer tarandus</i>	<i>Ursus americanus</i>	54	0.080	3
<i>Rangifer tarandus</i>	<i>Ursus arctos</i>	2	0.011	3
<i>Rangifer tarandus</i>	<i>Ursus arctos</i>	23	0.130	3
<i>Rangifer tarandus</i>	<i>Ursus arctos</i>	23	0.190	3
<i>Rangifer tarandus</i>	<i>Ursus spp.</i>	17	0.156	3
<i>Rangifer tarandus</i>	<i>Vulpes vulpes</i>	54	0.004	3
<i>Rangifer tarandus</i>	<i>Canis lupus</i>	65	0.060	2
<i>groenlandicus</i>				
<i>Ursus americanus</i>	<i>Lynx rufus</i>	68	0.043	3
<i>Ursus americanus</i>	<i>Puma concolor</i>	68	0.043	3

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