

# **Agent-based modeling of the dynamics of mammal-eating killer whales and their prey**

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## **Supplement: Design concepts and model details**

### **DESIGN CONCEPTS**

#### **Emergence**

System-level phenomena of primary interest were the population and group dynamics of killer whales and the population dynamics of prey. In particular, changes in the size and age-sex structure of the killer whale population in relation to changing prey numbers emerged from the model as adjustments to the maximum demographic rates that were imposed by the baseline schedules, while emergent prey dynamics resulted from killer whale predation imposed on the deterministic density-dependent dynamics of each prey population. Demographic consequences to killer whales were mediated by the predator-prey interactions and the energetics of prey consumption, body growth, and reproduction.

#### **Prediction**

The size of hunting groups of killer whales was controlled by a decision model that combined (or split) matrilineal groups of killer whales based on their anticipated success (amount of prey killed per whale) as a larger or smaller group. The actual numbers of prey to be encountered is unknown at the time of this decision, so the experience of the preceding day (number and kind of each prey encountered) was used as a prediction of prey encounters the following day, and the expected number killed (which was dependent on group size and prey species) was used to calculate comparative expectations for energy gain.

## **Interaction**

Individuals were assumed to interact in their hunting groups by sharing food proportional to the volume required to reach individual satiation (a combination of metabolic need and body condition). Interactions among groups of killer whales occurred at user-specified rates, with decisions made to combine or split matrilineal groups (or lone individuals) based on expected energetic return from hunting together or apart. Interactions between groups of killer whales and individual prey occurred during probabilistic encounters and resulted in prey being killed probabilistically according to modeled vulnerabilities of each prey type to hunting groups of that size.

## **Stochasticity**

Baseline demographic rates were generated by comparing values generated from a uniform (0,1) distribution to user-specified baseline probabilities of mortality and fecundity to determine the occurrence of daily mortality or annual conception events for each individual. The timing of conception was drawn from a normal distribution within the breeding season. Encounters between killer whales were generated daily from comparison of values from a uniform (0,1) distribution to the user-specified probabilities of encountering both a random group and a group of relatives. The actual group of relatives that was encountered was determined by weighting the probability of encounter for each group by the sum of past associations between the members of the 2 groups (see model details). Specified probabilities of encounter between a killer whale group and each prey were used to generate numbers of each prey from a binomial distribution ( $B(\text{encounter rate}, N)$ ), and the sequence of encounters was randomized. The outcome of each encounter (killed or not) was determined sequentially by comparison of values from the  $U(0,1)$  distribution to the modeled  $P(\text{killed}|\text{encounter})$ .

## **Collectives**

Killer whales were grouped into hunting groups of 1 or more based on mother-calf pair bonds and size-related advantages to the group for hunting the particular constellation of prey available at the time, as indicated by the previous day's encounters. Interactions with the prey (i.e. encounters and kills) took place at the hunting group level.

## **Observation**

Within each year, a sampling day (or days) was specified by the user to mimic data collection for the calculated output variables described in Table S1. The data represent all killer whales and prey in the population on that day or summary data for the intervening period since the last output. Output was written to comma-delimited text files that were used as input to spreadsheets or other analytical programs.

## **MODEL DETAILS**

The model is written in Repast, a Java-based software package for agent-based modeling (North et al. 2006). Output data are compiled on user-specified sampling dates and written to spreadsheet files for post-processing in spreadsheet or statistical software.

The model is executed in daily time steps (manuscript Fig. 1). At the beginning of each simulated day, whales hunt and feed. Once all feeding has occurred, metabolism and growth algorithms are applied, and demographic actions are taken. Finally, any changes in group membership for the following day are determined. Various flags are set to mark annually occurring events, such as birthing and sampling, for model output (Table S1). Running annual totals are kept of births, deaths, and prey consumption by killer whale age and sex class. Graphical output is provided during interactive computer runs, but practical running times are obtained only in batch mode, where pre-programmed commands control the program variables and output files that are analyzed after execution is complete.

The model is a work in progress; various upgrades and innovations in implementation may be found when consulting the documentation and downloads available at [www.math.uaa.alaska.edu/~orca/](http://www.math.uaa.alaska.edu/~orca/). Model code for the version presented here can be obtained at that site or from the authors.

### Initialization and input

Each model run was initialized from a batch parameter file specifying 3 input files that provided (1) the starting population of killer whales with their ages and the identity of their mothers, (2) baseline age-specific schedules of annual survival and conception probabilities with unlimited food, and (3) a file detailing parameters controlling prey body growth, energy content, density-dependent population dynamics, and predator-prey interactions. The batch startup file also allowed user control over model parameters that had programmed default values (Table S2).

### Submodels

#### Energetics

The requirements and efficiencies of converting prey or body mass into energy and using that energy to support field metabolic rate (FMR) or somatic production (Fig. 2 in the main article) are similar to those used by Winship et al. (2002) for Steller sea lions *Eumetopias jubatus*. We make the simplifying assumption of a constant ratio of lean to fat tissue in the body of killer whales with an average energetic value of 3.4 kcal g<sup>-1</sup>. Given that the metabolic rate of lean probably exceeds that of fat tissue, this may cause us to underestimate the metabolism of starving whales and overestimate that of well-conditioned whales, but this was considered an acceptable cost for simplifying the model, and its effect could be compensated for by adjustments in threshold values that control demographic consequences and by reducing metabolism when whales are starving. We allowed for decreasing metabolic rates by 50%, as seen in many marine mammal species (Worthy 2001), assuming a linear decline between user-defined thresholds (Table S2).

The energetics of modeled killer whales were based on the estimates of field metabolic rate (FMR) for delphinids (Williams et al. 2004):

$$\text{FMR} = 405.39 \times M^{0.756} \text{ kcal d}^{-1}$$

where  $M$  is the mass in kg. Metabolic and conversion efficiencies (Fig. 2 in the main article & Table S2) are similar to those suggested by Winship et al. (2002) and Moen et al. (1997, 1998), though few are based on killer whale studies, and many are poorly

known or unknown in marine mammals. Noren (2011) and Williams & Noren (2009) arrived at daily energy requirements of killer whales similar to those of Williams et al. (2004) but based on estimated activity states and costs of transport. The requirements for fetal growth and lactation, including the efficiencies in Fig. 2, are added to the female's FMR when determining the daily energetic maintenance requirements. The efficiency of supplying metabolic energy catabolized from tissues was assumed to be 0.8 (Barboza et al. 2009, their Table 10.1). The higher mass-specific energy generally needed by juveniles (Winship et al. 2002) is accounted for by explicitly modeling somatic growth and by the allometric parameterization of FMR (Williams et al. 2004).

### Body mass dynamics

Mass dynamics were based on a von Bertalanffy (1938) growth curve defining gender and age-specific target mass (Table S2). Asymptotic weights and growth rates were approximated from captive killer whales (Clarke et al. 2000), though these can be easily adjusted for newer data on other ecotypes (e.g. Williams et al. 2011). Body mass was regulated by reducing the amount of food consumed when an individual killer whale approaches or exceeds its age and sex-specific target mass. Our model assumes that a killer whale's maximum daily consumption (GutMassPercent) is a fixed proportion of its age and sex-specific Target Mass, somewhat greater than the daily rate of 4% reported for killer whales in captivity (Hoyt 1984). If an animal is underweight, we expect it would attempt to eat an amount near this maximum, and if very fat, would eat only as much as it takes to meet its daily metabolic requirements, including those for gestation and lactation demands. We estimated the proportion of a whale's maximum daily consumption that would be required to meet daily metabolic requirements and used the remainder to estimate the remaining gutfill that could be used to fuel body growth. We used a logistic function to describe the proportion of remaining gutfill that an animal would attempt to consume (i.e. beyond its metabolic needs) in relation to its actual mass/target body mass (Fig. S1). The mass of food required to meet this satiation level was based on the energy content of a preferred prey (harbor seals) rather than the energetic content of the diet on that particular day.

Killer whale calves transition gradually from milk to prey that are killed by its mother or other members of its pod or hunting group, probably within their first year (Heyning 1988). We assumed a logistic model ( $a = 6.1$ ,  $b = -0.02$ ) that reduced the proportion of milk in a calf's diet gradually from age 100 to 400 d. The energetic needs of the calf and food volume required for satiation were calculated using the same metabolic formula described for adults, with higher metabolism generated by the exponent of the field metabolic rate (FMR) and by requirements for body growth. The proportion of that target that was milk was used to calculate the energetic demand on the female as part of her daily energy requirement, and if she could provide it, the calf's diet included that energy. The remainder of the desired amount of food for the calf came from prey captured by the calf's hunting group, if available.

Growth of the fetus and associated maternal tissues is considered additional to the normal age-specific mass of a female. A general fetal growth model was used (Winship et al. 2002):

$$\text{Fetal Mass} = (\text{BirthMass}) / (1 + e^{a(t+b)})$$

where  $t$  is a proportion of total gestation length (510 d), BirthMass = 182,  $a = -15$ , and  $b = -0.68$ .

It is assumed that a pregnant female supports an additional mass (BirthMassLoss = 0.2) proportional to the fetus mass for placenta and blood that must be grown during pregnancy but is lost from her actual mass and target mass (TM) at birth. An additional parameter (PregnancyTissueMass) is allowed for mass gain that may occur in preparation for lactation following birth, but it is unknown if killer whales actually store energy for this purpose, and the default setting is 0.

### Killer whale demography

The model assumes underlying rates of conception and death that derive from causes unrelated to rates of prey consumption, as distinct from those that are mediated by the ability to maintain an expected body mass for that age and gender. These can be given as baseline probabilities of becoming pregnant or dying that yield maximum rates of growth with unlimited food. Olesiuk et al. (1990) suggest that the maximum rate of growth in resident killer whales is around  $\lambda = 1.04$ , and default values for this model (Fig. S2) are derived from their life table to produce such growth when prey are abundant. Individual mortality events were determined by comparing values from a uniform distribution to the daily probability of survival. Conception events were determined annually in the same way and then assigned to a conception date that year drawn from a normal distribution (Table S2). Conception rates rather than pregnancy rates from the literature were used because of the multiannual reproductive cycle, and the emergent calving rates were compared to Olesiuk et al. (1990) and unpublished data from C. Matkin.

The growth and consumption models described above produce individuals with variation in realized mass around that predicted from the age- and sex-specific growth curves, much as we see in natural populations. The model uses realized individual body mass to impose demographic consequences (e.g. births, deaths, aborted pregnancies, or termination of lactation) when the killer whale fails to maintain its mass above user-specified thresholds of its TM (Moen et al. 1997, 1998). The ability to maintain body mass is determined by the energetic requirements of the killer whales and their prey consumption. The parameters controlling thresholds (Table S2) are expressed as proportions of the age-specific TM of a whale and can be modified at the start of a simulation. Our default assumptions are that whales begin to starve at 0.90 of their TM, and their field metabolic rate declines to half normal in a linear fashion until starvation occurs at 0.7 of their TM. Similarly, milk production by lactating females is reduced linearly from its normal value to 0 as the female's mass falls from 0.85 to 0.75 of its TM (Table S2). Tissues associated with gestation (fetus and maternal tissue) are considered part of the female's TM additional to that calculated from her age-specific growth curve when setting mass-dependent satiation (but not GutMassPercent) levels.

### Killer whale group dynamics

We modeled the self-formation of groups based upon rules for aggregation and dispersal (Avilés et al. 2002, Parrish et al. 2002) to optimize a fitness function that explores the tradeoff between individual and group optimality. Because there is no spatial component that could be used to generate 'encounters' between groups, these are

generated probabilistically, with weighting toward groups that have a history of associations, such as near relatives. Our model allows approximate optimization of group size by maximizing the expected amount of prey each individual can expect to eat in a group while incorporating the effect of familial bonds that constrain the possible choices of hunting partners.

*The maternal unit.* Our model for social aggregation into hunting groups is based primarily on the mother-calf bond, which probably persists for female calves until they begin to reproduce and nearly indefinitely for male offspring unless an older brother is already present (Baird & Whitehead 2000). Dispersal of females occurs with the birth of their first calf (see demographics for age of first reproduction). For males in groups with an older male sibling already resident, dispersal occurs at sexual maturity, which defaults to 12.

*Histories of association.* Each model killer whale maintains a ‘memory’ of its past associations with all other killer whales. It is this history, rather than relatedness per se, that determines the probability of associating with a whale that is not its mother in the future. The effect is that siblings will tend to associate with their mother and with other siblings even after dispersal, but that those associations will be weaker with larger discrepancies in age.

The association memory is implemented by incrementing counters for all whales in a group during the daily time step. For example, consider 2 groups of whales shown below. Group 1 consists of 2 whales with IDs #1 and #2. Group 2 consists of 1 whale with ID #3. In Group 1, Whale #1 and Whale #2 have been in the same group for 150 time steps. Whale #1 and Whale #3 were previously in the same group for 20 time steps, although both whales are currently in different groups.

Group 1		Group 2	
Whale ID	Counters	Whale ID	Counters
1	3→20, 2→150	3	1→20
2	1→150		

If whale #1 has a newborn calf, then in the next time step, a counter for the calf will be added for all other whales in the group. Additionally, the counters are incremented for all whales in the group. This is shown below where the newborn is Whale #4.

Group 1	
Whale ID	Counters
1	3→20, 2→151, 4→1
2	1→151, 4→1
4	1→1, 2→1

If the calf is in the same exact group the next time step, then those counters will be incremented to 2. If at some point in the future a new whale joins the calf’s group, then a similar suite of new counters will be created for that whale that are initialized to 1. When a whale dies, the counters are removed. In this manner, each whale maintains a count of how frequently it has associated with other whales, which forms the basis from which whales can organize into hunting groups. A majority of these associations will be due to familial relationships.

*Hunting groups.* The grouping behavior of the whales affects the vulnerability of prey and ability to hunt certain types of prey. Field research indicates that 3 whales may be the optimal group size for smaller prey like harbor seals or harbor porpoises, while larger groups may be more effective for hunting gray whale calves (Baird & Dill 1995). Association of maternal groups with more extended family members is sometimes observed when transients are hunting and is likely related to the effectiveness of larger groups for certain types of prey, such as whales or large pinnipeds. We assume that there is an optimum group size for hunting each type of prey available to killer whales (described in the section ‘Predator–prey interactions’) and that the optimum group size at any time depends on the numbers of each prey type available.

If 2 groups are meeting based on association histories, then this group is chosen randomly with a weight proportional to the number of past associations of all group members. We compute the probability  $P(g_x, g_y)$  of group  $g_x$  encountering group  $g_y$  where whale  $w_i$  refers to a whale within a group we use:

$$Weight(g_x, g_y) = \sum_{w_x \in g_x} \sum_{w_y \in g_y} NumAssociations(w_x, w_y)$$

$$P(g_x, g_y) = \frac{Weight(g_x, g_y)}{\sum_{g_i \in AllGroups - g_x} Weight(g_x, g_i)}$$

An example is illustrated in Fig. S3, where we are trying to determine if Group 3 should meet with Group 1 or Group 2. Whales from Group 3 have interacted a total of 60 times with whales from Group 1 (Whale #4 has interacted 20 times with Whale #1, Whale #4 interacted 10 times with Whale #2, and Whale #5 interacted 30 times with Whale #2). Similarly, the whales from Group 3 have associated a total of 50 times with whales from group 2. As a result, Group 3 will meet Group 1 with probability (60/110) and will meet Group 2 with probability (50/110).

Two exceptions to these calculations are groups with mature males that have left their mother’s group due to an older sibling or females that have left their mother’s group due to the birth of a calf. The dispersal rules prevent these whales from joining their mother’s group, and in these cases, the mother’s group is removed from the calculations.

When 2 groups meet, they do not automatically join together. Only after 2 groups of whales have been selected that satisfy the encounter conditions do we evaluate whether or not the 2 groups will join together. Larger groups can more effectively hunt larger prey, but captured prey must now be shared among more group members. To optimize these competing factors, the model uses the larger of the 2 groups to determine the outcome by computing the expected amount of food per individual based on the vulnerability of the prey as a function of group size (see section ‘*Group-size dependent prey vulnerability*’). The list of prey used in this calculation is the actual prey that the group has encountered in the simulation the previous day, as opposed to the true number of prey that exists globally in the simulation, which amounts to an assumption of imperfect knowledge of the prey base and injects stochasticity to the optimization of group size. If this ‘energy’ value is larger in the combined group than the original group, then the 2 groups join together. Otherwise, no join occurs even if the smaller group might experience a larger energy gain by joining the larger group. This amounts to an

assumption of optimal foraging for the larger group, with constraints imposed by the size of the groups interacting (e.g. 2 groups of 3 can only form a group of 6 or remain separate on the day of their encounter).

In addition to accretion, a group will also consider whether or not it is advantageous to split into sub-groups on a daily basis. In this operation, the largest sub-group (what was once an original group that joined to form a larger group) computes whether the energy value will be optimized by remaining in the larger group or by splitting into its own group and selects the optimal choice. Conditions that may lead to this scenario include the death of whale(s), a change in the prey encountered, or a change in the group's composition based on the rules described in the section 'The maternal unit'.

We have implemented a model for groupings larger than the basic family unit by allowing smaller groups to combine together. As modeled here, the probability of a group of whales interacting with a different group each day is controlled by 2 stochastic variables chosen by the user: *ProbGroupsMeet* for the probability that a group of whales will meet another group of whales during the time step and *ProbJoinRandomGroup* for the probability that the group encountered is an arbitrary group of whales that may or may not have been associated together in the past. A uniform random number generator is used to generate these encounters. The number is generated per group, so it is possible for some groups to join and others to maintain their existing group structure during one time step. Note that *ProbGroupsMeet* is applied before *ProbJoinRandomGroup*. Only after it is determined that groups will meet is the decision made whether the group will be arbitrary or based on association histories.

Parameter *ProbGroupsMeet* sets the daily probability of one group encountering another group of killer whales. The parameter *ProbJoinRandomGroup* sets the probability that the group encountered and considered for partnership is a random group irrespective of past associations. This was considered a plausible but unlikely possibility based on literature accounts (Baird & Dill 1995, Baird & Whitehead 2000). A randomly selected group would be more likely to reflect the distribution of group sizes in the entire killer whale population, while the choices among those groups previously known would be more limited, reflecting the number of living relatives, their reproductive success, and their own particular hunting associations. We tested the sensitivity of group size to variation in *ProbGroupsMeet* while *ProbJoinRandomGroup* was held to 0 and varied *ProbJoinRandomGroup* while *ProbGroupsMeet* was held at 1 (*ProbJoinRandomGroup* only operates after a simulated encounter occurs, which depends on *ProbGroupsMeet* > 0). The effect of increasing the probability of encounters between groups with past histories was slightly positive but asymptotic (Fig. S4). The effect of increasing the probability that the groups meeting and joining would be unrelated was also positive and asymptotic, with a marked decline in the proportion of whales hunting alone (Fig. S4). The increasing standard deviation in group size across increasing values of *ProbGroupsMeet* and *ProbJoinRandomGroup* (Fig. S4) was an artifact of higher variability in killer whale population size, i.e. increasing mean group size to the optimum group size had the effect of increasing killing efficiency and raising population size and variability. Group size was greatest during periods of increase and smallest during population declines, leading to greater variability in mean group size as an artifact of



more variable population size. Adjusting encounter rates between predators and prey to control this effect showed that the effect of *ProbGroupsMeet* and *ProbJoinRandomGroup* on mean group size was robust. The mean group size counting all adults and juveniles was greater than the optimum based on ‘adult equivalents’ when these controlling parameters allowed the greatest model flexibility in joining groups, which was consistent with our expectations.

### Density-dependent prey populations

Models of the prey populations were constructed to be as simple as possible while incorporating features considered essential from the standpoint both of allowing different vulnerability of juveniles and adults and of incorporating realistic potential for density-dependent demographics. We considered the following elements to be essential to our prey populations:

- Density-dependent growth rates of marine mammals are expected to be non-linear, with maximum productivity declining rapidly near equilibrium (Eberhardt & Siniff 1977, Fowler 1981, Eberhardt 2002).
- The magnitude of density-dependent changes is likely to be greatest in juvenile survival, followed by adult reproduction, and be least in adult survival (Gaillard et al. 1998, Eberhardt 2002).
- Many prey species, including whales and large pinnipeds, are more vulnerable to predation by killer whales in their first year of life than as older animals (Heise et al. 2003, Wade et al. 2007).

All prey populations were modeled as 2 age-classes: ‘age 0 years’ and ‘adults’, with 3 density-dependent vital rates: a survival rate for each age class and per capita birth rate for the adult class. A Ricker function with 2 parameters ( $a$  and  $b$ ) was used for all 3 rates as a function of total prey population size,  $N$ :

$$\text{Rate} = \text{Max Rate} \times \exp(-aN^b).$$

All parameters in the model were defined at the annual rate, so that difference-equation models on a 1 yr time step could be used to generate plausible values and validate outputs; the 365th root of the calculated survival was used to model daily survival proportions, while the birth rate was applied on the species-specific birthing day annually. Maximum survival and birth rates were chosen to produce maximum population growth rates typical of particular species and life histories (e.g. ~1.12 for pinnipeds and small cetaceans, 1.08 observed of humpback whales) with adjustments to compensate for the fact that full age-sex structures were not being used (e.g. less than observed adult birth rates to account for pre-reproductive ages being included in the ‘adult’ model class). Similarly, density dependent parameters were chosen to produce the general pattern of maximum productivity at 70 to 75% of equilibrium and the greatest magnitude of changes in juvenile survival, birth rates, and adult survival, in that order (Fig. S5). All the parameters and prey populations used in the model are user-controlled and developed in an interactive spreadsheet (*PreyWorksheets.xls*, available in the download package online). Most simulations were conducted using a single or few prey species with parameters generating much larger populations of prey to compensate for the absence of the larger prey community that are known killer whale prey. These simpler

models were used to assess whether the model was producing realistic population-level behavior of killer whales under conditions of abundant or limiting prey and to compare the dynamics to classical models of a single predator and single prey species. Changes in prey vital rates and density dependence to simulate ‘regime shifts’ or extraneous ‘removals’ of known numbers to simulate human harvest can be input as options in the model during execution. The energy content of the prey consumed is specified in `prey.csv`, and while we have used values suggested in the literature, these might also be adjusted to account for differences in the cost to killer whales of pursuit and handling of different species and age classes.

### Predator–prey interactions

*Group-size dependent prey vulnerability.* While relatively little is known about the vulnerability of prey with age, greater vulnerability of juveniles is a common feature of predator–prey interactions, particularly as the size of the prey species relative to that of the predator becomes larger. In the case of transient killer whales, vulnerability of large whales is largely limited to calves (Wade et al. 2007), and there also appears to be greater vulnerability of Steller sea lion pups in comparison to older animals (Heise et al. 2003). This was considered an essential element to the prey model, while finer distinctions of sex and age were ignored. We also assumed that larger groups of killer whales would be more effective at killing prey, especially large prey, but the effect of sharing the prey in larger groups would produce an optimum group size for each prey type that produced the greatest amount of prey biomass per individual in the group (Baird & Whitehead 2000).

We implemented a model of killing rate similar to a classical formulation of attack rate  $\times$  number of prey, with attack rate partitioned into an encounter rate ( $e$ ), defined as the probability that a group of killer whales would encounter a particular individual prey, and vulnerability ( $v$ ) equal to the probability of being killed by the group once encountered (i.e. expected kills per day =  $e \times v \times$  number of prey available). To make this dependent on group size ( $x$ ), we used a simple logistic function (Fig. S6) with a user-defined maximum vulnerability and logistic parameters  $a$  and  $b$ :

$$v = \{v_{\max}[\exp(a + b)x]\} / [1 + \exp(a + b)x]$$

The logistic function was chosen for its generality and congruence with potential analyses of field data. Calf and juvenile killer whales are not as effective hunters as adults, so group size for this purpose was considered to be ‘adult equivalents’, where juveniles began a linear increase in hunting effectiveness at age 3 (HuntAgeMin equivalent to 0 adults) and were considered fully effective hunters at age 12 (HuntAgeMax equivalent to a single adult). Thus, a group of killer whales comprised of animals aged 1.5, 7.5, 24.5, 36.5 and 60.5 yr would have an effective group size of 3.5 for hunting purposes. We also linearly reduced the effectiveness of whales that become malnourished from full effectiveness to 0 effectiveness as metabolic rate declines (BeginStarve = 0.85 to EndStarve = 0.7, see section ‘Energetics’). Thus, a group of 2 adult killer whales in which one is at 0.95 of target mass and the other is at 0.75 of target mass would have an effective group size of 1.33. In this way, each age class of each prey species could be assigned plausible maximum vulnerabilities when encountered by a large group of killer whales, and differences in vulnerability with hunting group size could be modeled with a simple form that produces optimal predictions based on

individual gain per kill. Fig. S6 shows this relationship for a small prey species class, such as harbor seal adults, and for a large species class, such as gray whale calves. When adjusted for the size and energy value of particular prey and summed over all prey types available, the expected optimum group size for any suite of prey abundances can be calculated (and employed in choosing group sizes, as described earlier). This assumes no foraging specialization by killer whale groups, which we consider a baseline default assumption that might be studied later.

*Prey capture.* In executing a daily time step of foraging for a killer whale group, the model steps through all prey types to determine the number of prey encountered of each type, drawing random variables from a Poisson distribution with expectations equal to the product of  $e_i$  and the number of prey type  $i$ . Once all prey encounters are identified, their order is randomized, and each is subjected to a random trial to see if the encountered prey is killed by comparing its vulnerability (e.g. Fig S6) to a uniform random variable. The group kills prey in the list until the list is exhausted or enough prey are consumed to satiate all the individuals in the group. The kills are shared proportionally to the mass required for each killer whale in the group to satisfy its maintenance metabolic requirements and reach satiation.

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Table S1. Output variables from killer whale individual-based model (IBM) sampled on user-specified model days (usually annually on Day 243)

run number
year of simulation
day of sample
numbers of killer whales aged 0, 1, 2, 3–9 (sexes combined) and >9 yr (sexes separate) alive on sampling date
numbers of killer whales in same categories dying in interval between samples
number of female killer whales in pre-reproductive, reproductive and post-reproductive ages
number of pregnant killer whales
number of killer whales starving in interval
number of aborted pregnancies in interval
mean group size
number of each prey (juveniles, adults)
number of each prey killed in interval
mean body condition (actual/target body mass) of killer whales aged 0, 1, 2, 3–9 and >9 yr
mean number (and SD) of each prey type consumed by killer whales aged 0, 1, 2, 3–9 and >9 yr during interval
frequency distribution of daily hunting group sizes during interval

Table S2. User-specified parameters and files used in agent-based simulation model. Default parameter names and values are shown. Those not in separate input files had program default values that were modified in a batch start-up file

	<b>Killer whale model parameters</b>		
<b>Model compartment</b>	<b>Model component</b>	<b>Parameter or file name</b>	<b>Default value</b>
<b>Execution control</b>			
	Day of year that model variables are sampled for output	SampleDate	243
	Starting files and conditions for model execution	BatchFileName	batch.txt
	Run length	BatchRunLength	1
	Demographic rate file	Fileparameters	popparms.csv
	Starting population file	FilePopulations	population50.csv
	To control diagnostic messages	ShowDiagnostics	FALSE
	To suppress screen output	BatchMode	TRUE
	Prey populations and vulnerabilities	FilePrey	prey.csv
<b>Demographic</b>	Age-specific annual probabilities of conception	popparms.csv	
	Age-specific annual probabilities of survival	popparms.csv	
	Beginning age & sex structure, relatedness	population50.csv	
	Conception date	MeanDayPregnant	165
	Conception date standard deviation	StDevDayPregnant	35
	Gestation length (d)	DaysPregnancy	510
<b>Mass dynamics</b>			
	Von Bertalanffy asymptotic female mass	FemaleMaxMass	2700
	Von Bertalanffy growth exponent for females	FemaleVonBert	0.0003
	Von Bertalanffy asymptotic male mass	MaleMaxMass	4000
	Von Bertalanffy growth exponent for males	MaleVonBert	0.00025
	Proportion of target mass needed to maintain pregnancy	AbortionThreshold	0.75
	Mass of calf at birth	BirthMass	182
	Maternal mass gained, then lost at birth as proportion of calf mass	PregnancyTissueMass	0.2
	Proportion of target mass at which all lactation stops	LactationCease	0.75

	Proportion of target mass needed to maintain full milk production	LactationDecrease	0.85
	Extra mass gained during pregnancy to support future lactation	PregnancyWeightGain	0
	Proportion of target mass at which metabolism is reduced	StarveBeginPercent	0.9
	Proportion of target mass needed to avoid death by starvation	StarveEndPercent	0.7
	Fetal growth	BirthMass $\div (1 + e^{(a(t+b))})$	$a = -16, b = -0.68$
<b>Energetics</b>			
	Efficiency of energy conversion into fetal growth	EnergyToFetusEfficiency	0.2
	Efficiency of energy conversion into tissue growth	EnergyToMassEfficiency	0.8
	Efficiency of energy conversion into milk	EnergyToMilkEfficiency	0.75
	Field Metabolic Rate Constant (kcal)	FMRConstant	405.39
	Field Metabolic Rate Exponent (kcal)	FMRExponent	0.756
	Maximum daily prey consumption as proportion of target mass	GutMassPercent	0.055
	Efficiency of tissue catabolism for maintenance energy	MassToEnergyEfficiency	0.8
	Energy content of milk (kcal g <sup>-1</sup> )	MilkKcalPerGram	3.69
	Digestive efficiency of converting milk into energy	MilkToEnergyEfficiency	0.95
	Digestive efficiency of converting prey tissue into energy	PreyToEnergyEfficiency	0.85
	Caloric value of killer whale mass (kcal kg <sup>-1</sup> )	WhaleKcalPerKg	3408
<b>Group dynamics</b>			
	Daily probability of meeting another group of killer whales for hunting	ProbGroupsMeet	0.7
	Daily probability that group is unrelated	ProbJoinRandomGroup	0.1
<b>Predator-prey</b>	Prey population parameters (see text)	Prey.csv	User specified
	Predator-prey interaction parameters (see text)	Prey.csv	User specified
	Age killer whales reach full hunting effectiveness	HuntAgeMax	12
	Age juveniles begin to contribute to prey capture	HuntAgeMin	3
	Maintain constant annual prey population size for debugging	UseConstantPreyPopulation	False
	Starting population of juvenile prey	n 0	In Prey.csv
	Starting population of non-juvenile 'adult' prey	n adult	In Prey.csv
	Day of prey's annual birth pulse	BirthDate	In Prey.csv

Mass of juveniles at birth	n0_startmass	In Prey.csv
Mass of juveniles after 1 yr	n0_endmass	In Prey.csv
Mean mass of adult prey	ad_mass	In Prey.csv
Caloric value of juvenile prey	n0_kcal_gram	In Prey.csv
Caloric value of adult prey	ad_kcal_gram	In Prey.csv
Maximum birth rate of adults ( $>1$ yr)	BirthMax	In Prey.csv
Density dependent birth parameter $a$ in $\exp(-aN^b)$	Birth_a	In Prey.csv
Density dependent birth parameter $b$ in $\exp(-aN^b)$	Birth_b	In Prey.csv
Maximum juvenile survival	n0Surv_Max	In Prey.csv
Density dependent juvenile survival parameter $a$ in $\exp(-aN^b)$	n0Surv_a	In Prey.csv
Density dependent juvenile survival parameter $b$ in $\exp(-aN^b)$	n0Surv_b	In Prey.csv
Maximum adult survival	AdSurv_Max	In Prey.csv
Density dependent adult survival parameter $a$ in $\exp(-aN^b)$	AdSurv_a	In Prey.csv
Density dependent adult survival parameter $b$ in $\exp(-aN^b)$	AdSurv_b	In Prey.csv
Probability of encounter between killer whale group and juvenile prey	0_encounter_rate	In Prey.csv
Maximum vulnerability of juvenile prey to large killer whale groups	0_VulnMax	In Prey.csv
Logistic parameter $a$ for group-dependent vulnerability of juveniles	0_VulnA	In Prey.csv
Logistic parameter $b$ for group-dependent vulnerability of juveniles	0_VulnB	In Prey.csv
Probability of encounter between killer whale group and adult prey	ad_encounter_rate	In Prey.csv
Maximum vulnerability of adults to large killer whale groups	ad_VulnMax	In Prey.csv
Logistic parameter $a$ for group-dependent vulnerability of adults	ad_VulnA	In Prey.csv
Logistic parameter $b$ for group-dependent vulnerability of adults	ad_VulnB	In Prey.csv
Day of year prey become available to killer whales	Available_Start	In Prey.csv
Day of year prey become unavailable to killer whales	Available_End	In Prey.csv



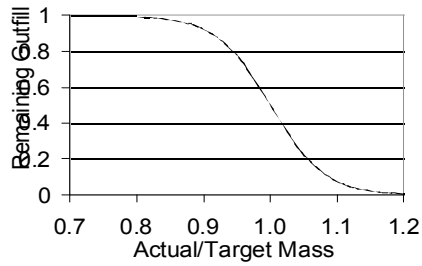


Fig. S1. Proportion of remaining stomach volume (beyond that needed for maintenance metabolism) that will satiate a model killer whale in relation to body condition (actual mass/target mass)

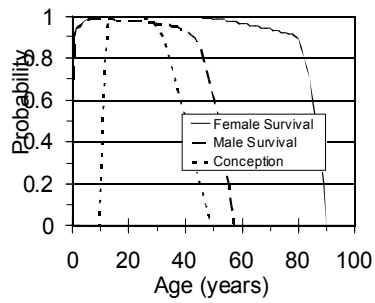


Fig. S2. Baseline annual probabilities of survival and conception for a population of transient killer whales unlimited by prey availability

Group 1		Group 2	
Whale ID	Counters	Whale ID	Counters
1	3→30, 2→150, 4→20	3	1→ 30, 4→20, 5→50
2	1→150, 4→10, 5→30		

Group 3	
Whale ID	Counters
4	1→ 20, 2→10, 3→20, 5→100
5	2→ 30, 3→50,4→100

Weight(Group 3, Group 1) = (20 + 10 + 30) = 60  
Weight(Group 3, Group 2) = (20 + 30) = 50

$P(\text{Group 3, Group 1}) = 60 / (60 + 50) = 55\%$   
 $P(\text{Group 3, Group 2}) = 50 / (60 + 50) = 45\%$

Fig. S3. Determining probabilities for group encounters. The model determines stochastically that Group 3 will encounter another group, then assesses the relative probability that the group encountered is Group 1 or Group 2 based on the sum of days counted in previous associations by all individuals in the groups (see text)

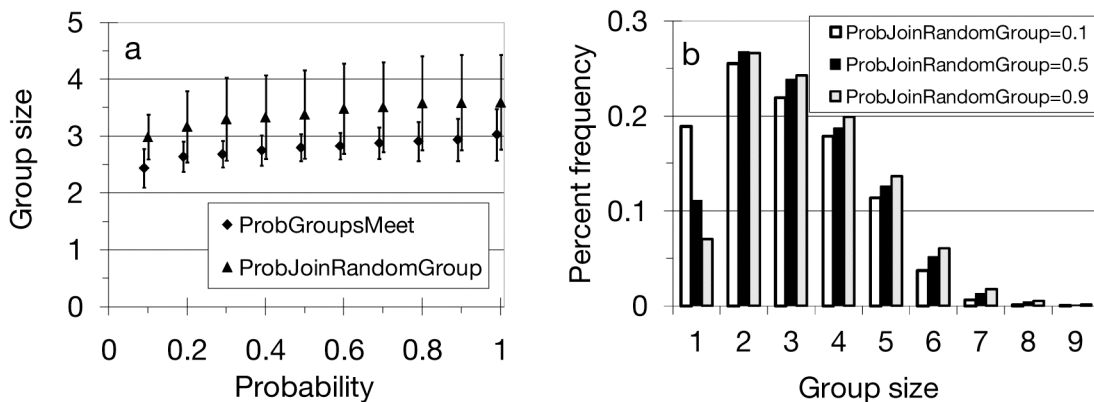


Fig. S4. (a) For an optimum hunting group size of 3, parameters controlling the daily probability of meeting and considering joining another group of killer whales (*ProbGroupsMeet*) and the probability that it would be a random group or a group of relatives (*ProbJoinRandomGroup*) had positive effects on the mean group size of hunting killer whales. (b) The increase in mean group size with increasing *ProbJoinRandomGroup* was accompanied by a marked decline in the proportion of whales hunting alone

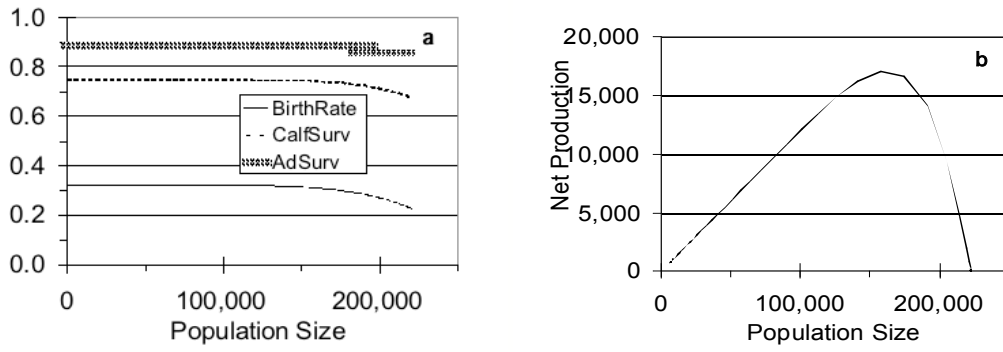


Fig. S5. General density-dependent properties of (a) vital rates and (b) net production ( $dN / dt$ ) of model prey populations

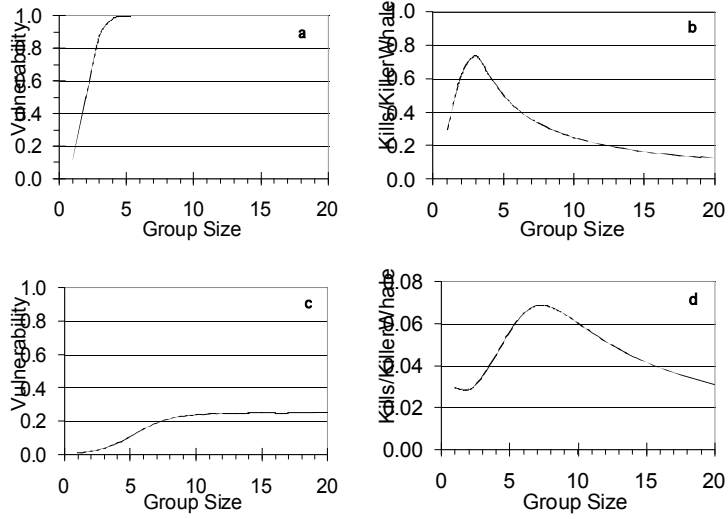


Fig. S6. (a,c) The modeled relationship between effective group size (in adult equivalents) of hunting killer whales and the probability of killing the prey given an encounter for (a) a relatively vulnerable prey (adult harbor seal) and (c) one less easily killed (gray whale calf). The paired graphs at right (b,d) show the resulting expectation of kills per whale in the group when the prey are shared