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East or west: the energetic cost of being a gray whale and the consequence of losing energy to disturbance

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METHODS

Gray Whale Female Energetic Demands

The duration of each of the adult female and calf stages were calculated based on migration distance, travel speed, and sighting information (Pike 1962, Rice & Wolman 1971, Sumich 1983, Withrow 1983, Braham 1984, Jones & Swartz 1986, Sumich 1986, Rodriguez de la Gala-Hernandez *et al*. 2008, Sychenko 2011, Mate *et al*. 2015). We assumed a mean birth date of Jan. 27 to estimate calf age at the different stages and weaning age (Rice et al. 1981, Withrow 1983, Jones & Swartz 1986), and that females with calves remained in the breeding lagoon for 70 days (Withrow 1983, Sumich 1986) in BajaC (Jones & Swartz 1986, Villegas-Amtmann et al. 2015). For WGW breeding in China we modeled two scenarios, in the first we assume that WGW remain in the China breeding grounds as long as possible, which is 365 days minus the time required to migrate to and from the breeding grounds plus the time spent on the feeding grounds, or 124 days. The second is that they remain in the breeding grounds for the same time as WGW migrating to BajaC, and that they take longer to migrate to and from the breeding lagoons which results in the same energy budget as WGW migrating to BajaC. We estimated a north migration duration of 101 days based on migration distance of 10,500 km from Laguna Ojo de Liebre, BajaC, Mexico to Sakhalin Island, Russia (Mate *et al*. 2015), and a north migration duration of 58 days based on migration distance of 5,969 km from Hainan Island, China to Sakhalin Island, Russia. Additionally, we considered the travel speed of mother-calf pairs of 4.32 km/hr (Rodriguez de la Gala-Hernandez *et al*. 2008), and observations of the first mother-calf pair at Piltun Lagoon on the northeastern coast of Sakhalin Island (Sychenko 2011) (O. Sychenko, [unpubl.]) .

Model Assumptions

Based on available literature we made the following model assumptions: (1) Under non-disturbance scenarios, females have the ability to acquire all the energy necessary for pregnancy and lactation (6.6 or 6.5 months) during the foraging period in which they are pregnant. When females with 5.4 or 5.3 month old calves arrive at the foraging grounds the following year, they still have sufficient stored energy to support their calf an additional 1.2 months. (2) Calves must nurse at least until they reach the foraging grounds to survive (at least 5.4 or 5.3 months of lactation), given that weaned calves are not observed during the northbound migration (L.K. Schwarz, [unpubl.]); (3) If females lack sufficient energy reserves to complete the southward migration (poor body condition), they will also lack the resources necessary to come into estrous and will not copulate that year. In that case, they will not become pregnant and will not have to support a growing fetus and a suckling calf. This would facilitate the acquisition of the necessary resources to become pregnant the following year; (4) There is no feeding outside of the foraging grounds; (5) Females can overwinter somewhere other than the breeding lagoons; (6) Female gray whales will prioritize resource allocation to their own survival and maintenance (metabolic rate) over calf maintenance and growth (lactation), and the latter over fetus maintenance and growth (pregnancy); (7) Females forage the maximum number of days possible given their reproductive state; (8) Females are capable of acquiring energy at the same rate during all foraging periods.

Lost Energy Predictions

1. Reproductive Condition A: Pregnant

For estimating consequences of disturbance when females are pregnant, we calculated the proportion of lost energy that would have the following consequences on the females' reproduction and survival: (a) wean the calf at a lower mass, (b) lose the fetus (abort), but become pregnant and calve the following year, (c) abort and not become pregnant, and therefore not calve the following year, and lastly (d) die. We assumed that if females do not acquire enough energy to complete lactation and the entire migration, they will not be able to become pregnant the following year. To estimate these costs we calculated the following:

- *1a) Female reproductive costs (RC):* total energetic requirement when females are pregnant (Reproductive Condition A) were calculated as:

$$RC = E_{Fg} + E_{Sb} + E_{Bl} + E_{Nb} + PC + LC \quad (1)$$

where E_{Fg}, E_{Sb}, E_{Bl}, and E_{Nb}, are the energy utilized at foraging grounds, while southbound, at the breeding lagoon and while northbound respectively; *PC* are pregnancy costs and *LC* lactation costs (for 6.6 or 6.5 months of lactation).

- *1b) Female reproductive costs for a lactation of 5.4 or 5.3 mo.* ($RC_{5.4\ or\ 5.3mo.}$): Minimum energy necessary to give birth and to wean a calf. Assuming that if a female is disturbed and does not acquire enough resources for a minimum lactation of 5.4 or 5.3 months (when female and calf reach the foraging grounds), the calf will not survive. Therefore:

$$RC_{5.4or5.3mo.} = RC - (LC \cdot propL_{Fg}) \quad (2)$$

where $propL_{Fg}$ is the proportion of lactation time at the foraging grounds (0.19-for both). Proportion of minimum energy for calf production was then calculated as $RC_{5.4or5.3mo.} / RC$.

- *1c) Female minimum reproductive costs (MRC):* Minimum energy required to survive and reproduce. Assuming that a female will abort early in the foraging season if she is not able to sustain pregnancy, but could be able to acquire enough energy to migrate and reproduce, and therefore, have a calf the following year. We estimated *MRC* as:

$$MRC = E_{Fg} + E_{Sb} + E_{Bl} + E_{Nb} \quad (3)$$

where E_{Fg}, E_{Sb}, E_{Bl} and E_{Nb} are the energy utilized when pregnant at foraging grounds, when non-pregnant while southbound and at the breeding lagoon and when pregnant while northbound. Proportion of minimum energy to survive and reproduce was then calculated as MRC / RC.

- *1d) Female minimum maintenance costs* for Reproductive Condition A (MC_{PA})*:* Assuming a female aborts early in the foraging season, and she is not able to acquire sufficient energy to migrate, reproduce and have a calf the following year. Therefore, a female would spend the winter outside the foraging grounds and breeding lagoons. To estimate minimum maintenance costs we used the lowest calculated FMR (measured during the northbound migration), for periods outside the foraging grounds. Female MC_{PA} was calculated as:

$$MC_{PA} = E_{Fg} + E_{Nb} \cdot d_{outFg} \quad (4)$$

where E_{Fg} is the energy required when pregnant at foraging grounds, E_{Nb} is the energy required when non-pregnant while northbound and d_{outFg} is the number of days outside foraging grounds during the year in which she is (was) pregnant. Then, we calculated the proportion of minimum energy necessary for a female's own maintenance for Reproductive Condition A, below which a female would not survive, as MC_{PA} / RC . This assumes that a female will die if she cannot meet her minimum maintenance energy requirements. We know this is not the case as females can utilize body tissues going into negative energy balance before they die, and thus we assumed the most conservative worst case scenario.

2. Reproductive Condition B: Resting (non-pregnant, not lactating)

This prediction assumes that due to disturbance during the previous year, a female did not have enough energy to sustain her pregnancy (aborted) or to migrate and become pregnant. Therefore, she is non-pregnant and without a calf when she returns to the foraging grounds. Lost energy during this reproductive condition would have the following consequences on a female: (a) not being able to migrate and breed again (does not have a calf for another year, extending her breeding cycle an additional year), and (b) die. We assumed that if females do not acquire enough energy to complete the entire migration, they will not be able to reproduce. To estimate these costs, we calculated the following:

- *2a) Female reproductive costs* for Reproductive Condition B *(RC_B):* total energetic requirements when females are non-pregnant (Reproductive Condition B) were calculated as:

$$RC_B = E_{Fg} + E_{Sb} + E_{Bl} + E_{Nb} \quad (5)$$

where E_{Fg}, E_{Sb}, E_{Bl} and E_{Nb} are the energy utilized when non-pregnant at the foraging grounds, while southbound, at the breeding lagoon and while northbound respectively. Proportion of energy needed to survive and reproduce was then calculated as $RC_B \;/ RC$.

- *2b) Female minimum maintenance costs* for Reproductive Condition B (*MC_{PB}*), and proportion of minimum energy necessary for a female's own maintenance, below which a female would not survive were calculated as in Reproductive Condition A.

3. Reproductive Condition C: Lactating

This prediction assumes that if disturbed during the previous foraging period, when a female was pregnant, she may not have acquired all of the energy necessary to complete lactation. Therefore, once she has successfully brought the calf to the foraging grounds she may need to acquire the energy necessary for 1.2 months of lactation at the foraging grounds. Lost energy during lactation would have the following consequences on a female: (a) not become impregnated the following year, (b) wean the calf at a lower mass and (c) die. We assumed that if females do not acquire enough resources to complete the current lactation and entire migration, they will not be able to reproduce, as they will forego the next breeding event before sacrificing their lactating calf. To estimate these costs, we calculated the following:

- *3a) Female reproductive costs* for Reproductive Condition C *(RC_C)*: total energetic requirements when females are non-pregnant + the proportion of lactation costs at the foraging grounds (*$propL_{Fg}$*) (19% of total lactation costs) were calculated as:

$$RC_C = E_{Fg} + E_{Sb} + E_{Bl} + E_{Nb} + (LC \cdot propL_{Fg}) \quad (6)$$

Then, we calculated the proportion of foraging time below which a female will not reproduce as:

$$RC_C / [(RC \cdot D_{Fg2}) / D_{Fg1}] \quad (7)$$

where D_{Fg2} = 134 or 148 days, is the amount of time a female spends at the foraging grounds when she has a calf, and is shorter than D_{Fg1} = 192 or 197, the time spent at the foraging grounds when she has no calf, either pregnant or not. That is, because lactating females remain longer at breeding lagoons, arriving later at the foraging grounds, compared to single females.

- 3b) *Female minimum costs to wean a calf at a normal mass (no reproduction) (WC):* Assuming a female was not able to acquire the energy necessary for migration in addition to lactation (she was not able to reproduce and will not have a calf the following year, getting into a 3 yr. breeding cycle) and spends the winter outside the foraging grounds and breeding lagoons. To estimate minimum costs for weaning a calf at a normal mass, we used the lowest calculated FMR for periods outside the foraging grounds, as in Reproductive Condition A-1d. We calculated *WC* as:

$$WC = E_{Fg} + E_{Nb} \cdot d_{outFg} + (LC \cdot propL_{Fg}) \quad (8)$$

Where E_{Fg} is the energy utilized when female has a calf at foraging grounds E_{Nb} is the energy utilized when she is non-pregnant while northbound, d_{outFg} is the number of days outside foraging grounds during a year in which she had a calf. Proportion of energy needed to wean a calf at 6.6 or 6.5 months, below which the calf is weaned at a lower mass was then calculated as:

$$WC / [(RC \cdot D_{Fg2}) / D_{Fg1}] \quad (9)$$

- 3c) *Female minimum maintenance costs* for Reproductive Condition C (MC_{PC}): Assuming a female was not able to acquire the energy necessary for 1.2 months of lactation or migration (her calf would be weaned at a lower mass and she will not reproduce, getting into a 3 yr. breeding cycle). Female MC_{PC} was calculated as:

$$MC_{PC} = E_{Fg} + E_{Nb} + d_{outFg} \quad (10)$$

where E_{Fg} is the energy utilized when a female has a calf at the foraging grounds, E_{Nb} is the energy needed when she is non-pregnant while northbound and d_{outFg} is the number of days outside foraging grounds during the year in which she had a calf (as in Reproductive Conditions A-1d and C-3b above). We calculated the proportion of minimum energy necessary, below which a female would not survive, for Reproductive Condition C, as:

$$MC_{PC} / [(RC \cdot D_{Fg2}) / D_{Fg1}] \quad (11)$$

Population Model Linking Lost Energy to Reproduction and Survival

Pseudo-code for determining population results of lower net energy intake

Initialization

1) Assign number of adult females (nFem = 200 for our example)

2) From posterior sample of the bioenergetics model, draw nFem adult female masses and the corresponding caloric cost of

i) survival (E_s),

ii) migration (E_m),

iii) pregnancy (E_p),

iv) and early and late lactation (E_l_e, E_l_l).

3) Calculate the maximum amount of energy needed for each individual in each state (MaxEnergy):

  i) Pregnant: E_s + E_m + E_p + E_l_e

  ii) Lactating: E_s + E_m + E_l_l

  iii) Resting: E_s + E_m

4) Determine starting proportion of females in each reproductive state

  i) random draw from Cooke (2010) survival and reproductive rates (beta distributions with given means and variances)

  ii) dominant eigenvector of the Leslie matrix

5) Randomly assign starting reproductive state for each female based on proportions

6) Assign initial energetic reserves for each individual (ResEnergy = 0 for our example)

7) Assign proportion of energy allowed to acquire during feeding season (PropEnergy = 0.95 to 0.35 in increments of 0.05 for our example)

8) Assign number of years for projection (nYrs = 100 for our example)

For each year:

1) For each individual:

  i) Determine the total amount of energy acquired for the year (TotEnergy = ResEnergy + MaxEnergy*PropEnergy)

  ii) Female is assigned a new state for the next year based on the total amount of energy she has and the state she was in

  (a) Pregnant ->

    1. Lactating (TotEnergy >= E_s + E_m + E_p + E_l_e)
    2. Pregnant (E_s + E_m <= TotEnergy < E_s + E_m + E_p + E_l_e)
    3. Resting (E_s <= TotEnergy < E_s + E_m)
    4. Dead (TotEnergy < E_s)

  (b) Lactating ->

    1. Pregnant, normal calf wean mass (TotEnergy >= E_s + E_m + E_l_l)
    2. Resting, normal calf wean mass (E_s + E_l_l <= TotEnergy < E_s + E_m + E_l_l)
    3. Resting, lower calf wean mass (E_s <= TotEnergy < E_s + E_l_l)
    4. Dead (TotEnergy < E_s)

  (c) Resting ->

    1. Pregnant (TotEnergy >= E_s + E_m)
    2. Resting (E_s <= TotEnergy < E_s + E_m)
    3. Dead (TotEnergy < E_s)

  iii) Update reserve energy. ResEnergy = TotEnergy - minimum amount needed for transition to new state.

2) Calculate number of calves weaned at lower mass/total number of calves.

3) Calculate annual reproductive rate: number of lactating females/total number of live females in same time step.

4) Calculate annual adult female survival rate: number of live females/total number of females alive in the previous time step.

5) Calculate mean and 95% posterior interval of surviving female mass.

6) Repeat for nYrs.

To estimate distributions, the above can be repeated many times (nIter = 500 for our example)

Stable rates

1) Determine stable reproductive rate: mean and 95% posterior interval for combined reproductive rate, nYrs = 40 to 100 for all iterations

2) Determine stable proportion of calves weaned at a lower mass: mean and 95% posterior interval for combined proportion at lower wean mass, nYrs = 40 to 100 for all iterations

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