Using Group Composition as a Predictor of Feeding and Travelling Bout Lengths in Norwegian Killer Whales (*Orcinus orca*)

Lorenz Gygax

Applied Mathematics, University of Zürich, LGygax@proximate-biology.ch

*Gygax, L. (2000) Using Group Composition as a Predictor of Feeding and Travelling Bour Lengths in Norwegian Killer Whales (*Orcinus orca*). Available on http://www.proximate-biology.ch/lgygax/phd/info.html:*

Feeding and travelling bout lengths in killer whales were investigated for their dependence on group size and group composition (proportion of calves/juveniles, proportion of males). Feeding bouts last longer in the presence of calves/juveniles and in larger groups. Travelling bout length is not affected by group size nor group composition. These patterns can be accounted for either by a switch of foraging strategies, by intragroup competition or by the cost of raising young.

To secure survival and reproduction animals have basic energetic needs. This is no different for dolphin species. The needs differ between individuals of different sizes, e. g. the sexes in dimorphic species such as killer whales, *Orcinus orca* (Kriete, 1995), and of different reproductive status, e. g. lactating females which need more energy than other females (Kastelein *et al.*, 1993; Kriete, 1995). This becomes visible in the study of energetics (Kriete, 1995) and the study of feeding behaviour where lactating females have a different diet composition (e. g. Bernard and Hohn, 1989; Cockcroft *et al.*, 1993; Nishiwaki and Handa, 1958; Robertson and Chivers, 1997; Young and Cockcroft, 1994), feed on larger prey (e. g. Recchia and Read, 1989; Yasui and Gaskin, 1986) or feed for longer time periods. (e. g. Robertson and Chivers, 1997; Yasui and Gaskin, 1986)

It is therefore surprising, that a strongly dimorphic species such as the killer whale forms very stable family pods (Bigg *et al.*, 1990, and most likely in Northern Norway, Similä, personal communication) that only seem to split rarely into clearly defined age–sex classes. How can the animals of the different age–sex classes in such a pod accommodate their own energetic needs?

If the cooperation of *all* pod members for hunting herring were not crucial, it would be most likely that even killer whale family pods would split into subpods according to age and sex, in such a way that individual energy requirements would be met by all members of the pod. The aim of the current study was to determine whether such intra–pod splits occur, to specify which age–sex classes formed subpods and to investigate the behaviour of the subpods in relation to their composition.

Unfortunately, killer whales were more rarely encountered than had been expected, and could not be followed over longer time periods; hence hardly any splits were actually observed. Only feeding and travelling groups were observed. I thus attempt to evaluate the dependence of the duration of feeding and travelling bouts on group size and on age–sex composi-

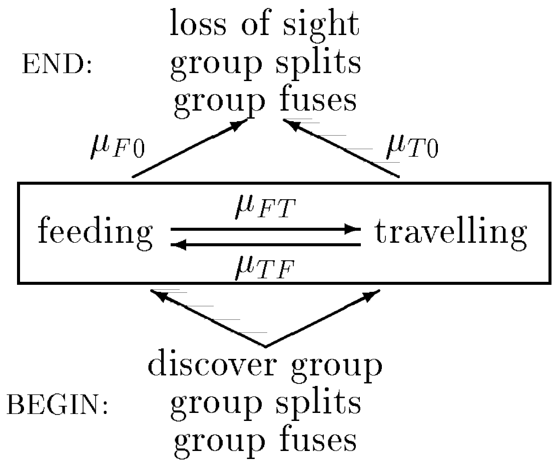

Figure 1: Observations for each group seen as a Markov chain. Feeding and travelling are continuous; all other states are instantaneous. The continuous box indicates the part which would ideally be modelled. See text for further explanation.

tion of the group. This should give an indication of how groups of different compositions adjust their time–allocation to these two important behavioural categories.

Methods

Observations were conducted from November 3rd to December 15th, 1997, in the area of Tys- and Vestfjord in Northern Norway. Observers were stationed on elevated points on land using telescopes and binoculars and in a 5 m aluminium boat with an 80 hp outboard engine.

A group was assumed to consist of all individuals that could be clustered according to single linkage (nearest neighbour) based on spatial distance, with a threshold of 1 km. But other cluster rules could also have been used since killer whales always formed "true" groups.

Each individual was attributed to one of three classes: (1) adult males: disproportionally high backfin, (2) calves/juveniles: small radius while breathing and up to one third of the length of adult males, (3) adult females and subadult males (all others).

During these observations, the two behaviours travelling (directed movement for longer than one minute at constant speed) and feeding (stationary and diving in different directions with bodies heavily arched) could be observed. The flow chart in Fig. 1 describes all behavioural sequences that were observed.

As soon as killer whales were sighted, they were assigned to groups as described above. As many groups as could be continuously tracked were chosen as focal groups. For each of these groups, the following information was noted: date, location, number of animals in the three classes defined above and the sequence and duration of the two behaviours, rounded to the next full minute.

These focal groups are considered to be statistically independent for the following evaluation, even though the same pod might have been in focus several times.

Differences in bout length were investigated by analysing the transition rates (which are inversely proportional to the bout lengths) between the two behaviours. The size of a group, the proportion of juvenile/calves and the proportion of males in a group were taken as possible explanatory variables.

The observations can be modelled as a simple continuous time Markov chain (Fig. 1). If it is assumed that the duration of the behavioural states is exponential, there is no need to consider what happened before the observations began, because of the lack of memory of an exponential distribution (e. g. Haccou and Meelis, 1994, , p. 13)

The prime interest in the present study was to estimate the transition rates between travelling and feeding (μ_{FT} and μ_{TF}, Fig. 1). This was accomplished by considering the transitions between feeding and travelling as true observations (the continuous box in Fig. 1) and by treating the transitions to the end states as censored data which could together be subjected to a survival analysis.

Unfortunately, there were only very few ob-

Table 1: Observed feeding bouts, estimated transition rates to travelling and binomial tests of occurrences of transitions.

	group size		proportion of calves/juveniles		proportion of males	
	< 5	≥ 5	$= 0$	> 0	$< 1/3$	$\geq 1/3$
number of bouts	9	10	12	7	8	11
total duration [min] [a]	126	290	143	273	288	128
number of transitions [b]	5	2	6	1	3	4
rate of transitions [c]	0.040	0.007	0.042	0.004	0.010	0.031
rel. transition intensity [d]	5.75		11.45		3.00	
Binomial probability [e]	$\mathbf{P}[Bi(7, 0.70) \leq 2]$		$\mathbf{P}[Bi(7, 0.66) \leq 1]$		$\mathbf{P}[Bi(7, 0.69) \leq 3]$	
p–value	0.030		0.008		0.136	

[a] T_1, T_2 [b] n_1, n_2 [c] $\mu_1 = n_1/T_1$, $\mu_2 = n_2/T_2$ [d] $\max(\mu_1, \mu_2)/\min(\mu_1, \mu_2)$ [e] $\sim Bi(n_1 + n_2, T_k/(T_1 + T_2))$, k such that n_k minimal

served transitions between the two behavioural states (7 from feeding to travelling and 4 from travelling to feeding). In such a case, it must be expected that estimates from a survival analysis based on asymptotic χ^2 distributions are not very reliable and therefore a simpler evaluation was performed.

If an explanatory variable was categorical with two states x_1 and x_2 we can split our observations (either the ones on feeding or the ones on travelling) into these two groups and sum the total duration in state 1 and state 2, T_1 and T_2. We can also count the number of transitions that occurred from state 1 and 2, n_1 and n_2.

Under the assumption that the durations in a behavioural state are exponentially distributed, we then know that n_1 is sampled from a Poisson distribution $Po(\lambda_1 T_1)$ and n_2 from $Po(\lambda_2 T_2)$, where the λ_i are the state specific transition rates. The test for $\lambda_1 = \lambda_2$ is equivalent to that of the null hypothesis that n_1 is a sample from the binomial distribution $Bi(n_1 + n_2, T_1/(T_1 + T_2))$.

This analysis was performed separately for the observations of feeding durations and travelling durations. Given that very few transitions were observed, the explanatory variables (group size, proportion of calves/juveniles and proportion of males) were dichotomised around their median value (see Tables 1 and 2 and 3) and only subjected to univariate tests.

The binomial probabilities that are calculated in this analysis are one–sided from asymmetric binomial distributions. Thus, to reach the 5 % statistical significance of a two sided–test they should be smaller than 2.5 % following the approach suggested by Cox and Hinkley (1974, p. 106; not considering that multiple tests were run).

There was one extremely long observation of feeding behaviour. For this reason the evaluation of the feeding bout durations was conducted twice, once with the original data and once where this extreme value was replaced by the next higher value (45 minutes instead of 150).

The summary statistics and binomial probabilities were calculated with R Version 0.63.1 (see http://www.r-project.org) on a SuSE Linux 5.2 system.

Results

In total, 31 groups of a median size of 4 individuals (range: 1 to 15) were observed for a median length of 15 minutes (range: 2 to 150). The groups consisted of a median of one third males (range: 0 to 100 %) and 0 % calves/juveniles (range: 0 to 25 %). 19 of the groups could be observed while feeding and 23 while travelling.

Transition rates from feeding to travelling

Table 2: Observed feeding bouts when the length of the outlier is reduced, estimated transition rates to travelling and binomial tests of occurrences of transitions.

	group size		proportion of calves/juveniles		proportion of males	
	< 5	≥ 5	$= 0$	> 0	$< 1/3$	$\geq 1/3$
number of bouts	9	10	12	7	8	11
total duration [min]	126	185	143	168	183	128
number of transitions	5	2	6	1	3	4
rate of transitions	0.040	0.011	0.042	0.006	0.016	0.031
rel. transition intensity	3.67		7.04		1.91	
Binomial probability	$\mathbf{P}[Bi(7, 0.59) \leq 2]$		$\mathbf{P}[Bi(7, 0.54) \leq 1]$		$\mathbf{P}[Bi(7, 0.59) \leq 3]$	
p–value	0.101		0.040		0.313	

Table 3: Observed travelling bouts, estimated transition rates to feeding and binomial tests of occurrences of transitions.

	group size		proportion of calves/juveniles		proportion of males	
	< 4	≥ 4	$= 0$	> 0	$\leq 1/3$	$> 1/3$
number of bouts	10	13	18	5	12	11
total duration [min]	131	123	184	70	45	209
number of transitions	1	3	3	1	0	4
rate of transitions	0.008	0.024	0.016	0.014	0.000	0.019
rel. transition intensity	3.20		1.14		∞	
Binomial probability	$\mathbf{P}[Bi(4, 0.52) \leq 1]$		$\mathbf{P}[Bi(4, 0.28) \leq 1]$		$\mathbf{P}[Bi(4, 0.18) \leq 0]$	
p–value	0.289		0.694		0.458	

groups including calves/juveniles) search for and choose larger patches of food (longer travelling bouts) or that groups of different age–sex composition follow different strategies.

This is in contrast to observations in the northeastern Pacific where there seems to be a difference between the sexes; there males seem to separate from family groups to feed alone in small groups, possibly increasing their efficiency (Hoelzel, 1993).

Calves/juveniles neither elongate travelling bouts by their slower swimming speed nor shorten them by their lower endurance. Efficient "transport" of the young members of a group might be reached if they travel in the echelon position.

From the present data, it is difficult to tell whether groups of different compositions switch their optimal foraging strategy, or whether we just witnessed a more proximate result of the costs of grouping or of raising young.

The details and causes of the patterns that emerged in the present study can only be addressed with the aid of more detailed observations of the formation of subgroups, the individual membership of such subgroups and their detailed foraging behaviour (including information on the patch sizes that are used and that are available). This can only be accomplished by long–term focal observations of individually known whales.

Acknowledgements

I would like to thank L. and A. Gygax for their interest in my work and some financial support, P. Baumann, D. Späni and S. Stöckenius for their help in gathering the data in the field and some preliminary evaluations, T. Similä, H. Hveding, P.–O. Lund, O. Breivik, K. Mathisen for hospitality and other goodies in the field, A. D. Barbour for clarifying the manuscript and for statistical help and D. C. Turner for correcting my English. Part of the evaluation and writing of this paper was supported by grants Nr. 20-43'453.95 and 20-50'686.97 of the Swiss National Science Foundation.

References

Bernard, H. J. and Hohn, A. A. (1989). Differences in feeding habits between pregnant and lactating spotted dolphins (*Stenella attenuata*). *Journal of Mammalogy*, **70**, 211–215.

Bigg, M. A., Olesiuk, P. F., Ellis, G. M., Ford, J. K. B., and Balcomb, K C, I. (1990). Social organization and genealogy of resident killer whales (*Orcinus orca*) in the coastal waters of British Columbia and Washington state. In P. S. Hammond, S. A. Mizroch, and G. P. Donovan, editors, *Individual Recognition of Cetaceans: Use of Photo–Identification and Other Techniques to Estimate Population Parameters*, volume 12 of *International Whaling Commission Special Issue*, pages 383–405. The International Whaling Commission, Cambridge.

Bisther, A. and Vongraven, D. (1994). Presence of "baby–sitting" males among Norwegian killer whales (*Orcinus orca*): Alloparental behaviour as an indicator of social complexity. *European Research on Cetacea*, **7**, 24–25.

Cockcroft, V. G., Haschick, S. L., and Klages, N. T. W. (1993). The diet of risso's dolphin *Grampus griseus* (Cuvier, 1812), from the east coast of South Africa. *Zeitschrift für Säugetierkunde*, **58**(5), 286–293.

Cox, D. R. and Hinkley, D. V. (1974). *Theoretical Statistics*. Chapman and Hall, London.

Creel, S. (1997). Cooperative hunting and group size: Assumptions and currencies. *Animal Behaviour*, **54**(5), 1319–1324.

Haccou, P. and Meelis, E. (1994). *Statistical Analysis of Behavioural Data*. Oxford University Press, Oxford.

Hoelzel, A. R. (1993). Foraging behaviour and social group dynamics in Pudget Sound killer whales. *Animal Behaviour*, **45**, 581–891.

Kastelein, R. A., McBain, J., Neurohr, B., Mohri, M., Saijo, S., Wakabayashi, I., and Wiepkema, P. R. (1993). The food consumption of Commerson's dolphins *Cephalorhynchus commersonii. Aquatic Mammals*, **19**(2), 99–121.

Kriete, B. (1995). *Bioenergetics in the Killer Whale,* Orcinus orca. Phd, University of British Columbia.

Lee, P. C. (1994). Social structure and evolution. In P. J. B. Slater and T. R. Halliday, editors, *Behaviour and Evolution*, pages 266–303. Cambridge University Press, Cambridge.

Nishiwaki, M. and Handa, C. (1958). Killer whales caught in the coastal waters off Japan for recent ten years. *Scientific Reports of the Whales Research Institute, Tokyo*, **13**, 85–96.

Recchia, C. A. and Read, A. J. (1989). Stomach contents of harbour porpoises *Phocoena phocoena* L. from the Bay of Fundy Canada. *Canadian Journal of Zoology*, **67**(9), 2140–2146.

Robertson, K. M. and Chivers, S. J. (1997). Prey occurrence in pantropical spotted dolphins, *Stenella attenuata*, from the eastern tropical Pacific. *Fishery Bulletin*, **95**(2), 334–348.

Similä, T. and Ugarte, F. (1993). Surface and underwater observations of cooperatively feeding killer whales in northern Norway. *Canadian Journal of Zoology*, **71**(8), 1494–1499.

Waite, J. M. (1988). *Alloparental Care in Killer Whales (*Orcinus orca*)*. Masters, University of California, Santa Cruz.

Yasui, W. Y. and Gaskin, D. E. (1986). Energy budget of a small cetacean, the harbour porpoise, *Phocoena phocoena* (L.). *Ophelia*, **25**, 183–197.

Young, D. D. and Cockcroft, V. G. (1994). Diet of common dolphins (*Delphinus delphis*) off the south–east coast of Southern Africa: Opportunism or specialization? *Journal of Zoology, London*, **234**(1), 41–53.