

Correlates of Surface Behaviour in Norwegian Killer Whales (*Orcinus orca*)

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*Gygax, L. (2000) Correlates of Surface Behaviour in Norwegian Killer Whales (Orcinus orca). Available on <http://www.proximate-biology.ch/lgygax/phd/info.html>: In the present study correlates of surface behaviours such as tailslaps, spyhops and leaps were investigated in killer whales (*Orcinus orca*). Tailslaps were correlated with feeding, big group sizes and with an increasing proportion of adult males. This is interpreted as part of the feeding behaviour but a social role cannot be excluded. The number of spyhops increased with decreasing group size, while feeding and with decreasing proportion of adult males. This might indicate that spyhops are important in the coordination of several small groups of females while (possibly) feeding cooperatively. Leaps seemed to depend on group size and possibly weakly on the proportion of males in a group. This is suggestive of a social function. But if we really want to understand these surface behaviours it is necessary to develop a method that allows continuous focal observations of individual orcas and other dolphinids.*

Most scientists studying the behaviour of cetaceans have to confine themselves to what they see at the surface. Behaviours shown at the surface like tailslapping, spyhopping or leaping are very striking in contrast to respiratory surfacings.

Many hypothesis have been proposed on the functions of these surface behaviours:

Tailslap. In northern Norway tailslaps may mainly occur during the hunting of herring as a means of stunning prey (Similä, 1997; Similä and Ugarte, 1993). Sooten (1994) has proposed that tailslaps in Hector's dolphins form part of intragroup aggressive displays occurring simultaneously with biting and chasing. The function of the tailslaps may vary with context (rest, play, hunting, foraging) but is seen as either a signal or to frighten fish (Jacobson, 1986).

Thus tailslaps should either occur mainly during feeding or during social interactions. If

tailslaps have a social function, it can be postulated that they occur in clusters, as animals exchange aggressive interactions once such a behavioural bout has been initiated. I. e., if there is an aggressive interaction, several tailslaps should occur within a short time with longer periods between such interactions.

Spyhop. Sooten (1994) observed spyhops in Hector's dolphins mainly in conjunction with sexual behaviour but also small spyhops (chin-out) while feeding. Jacobson (1986) reports the greatest frequency of spyhops during resting and play, but also attributes a function of above-surface scanning of the environment to it, be it towards boats or shores. Visual orientation might become necessary especially when acoustic orientation is disturbed e. g. by the vicinity of boats but would not be useful if sight is reduced by weather conditions (mist). Exploration would mainly make sense if the behaviour was shown close to an object of interest

(e. g. a boat) and/or was performed mainly by juvenile animals.

Leap. Slooten (1994) observed leaps of Hector's dolphins to be most closely connected with aggressive and sexual behaviour. Another hypothesis attributes a (long-range) communicative function to the leaps as the splashes are assumed to be heard over a long distance and can occur while a pod is feeding (Jacobson, 1986).

Würsig (1986) differentiated three types of leaps that occurred during dusky dolphin feeding. At the beginning of a foraging bout he observed steep leaps with smooth entry that might allow for quick dives after breathing; later while feeding dolphins made splashing leaps which might attract other groups of dolphins to help herding sardine swarms at the surface; and finally, after feeding acrobatic leaps could be observed which most likely have some sort of social function.

Thus leaps are primarily assumed to either occur in a social context or when information needs to be transmitted. Especially if the leaps are a form of dominance signal, it might also be assumed that they occur in clusters and that they are predominantly shown in an age-sex class where rank is most important (presumably adult males).

In this study the occurrence of surface behaviours in orcas in dependence upon group composition, group behaviour and ecological variables is investigated.

Methods

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

A "group" was defined to consist of all individuals "connected" in a net if one could con-

nect them with each's nearest neighbour and they were all within an area of approximately 1 km². If group composition changed, a new group was protocolled. Within such groups data were summed for all group behaviours shown (see below).

The observational units (called "units" from here onwards) based on these focal groups and group behaviours are assumed to be statistically independent for the following evaluation, even though the same pod (and for different behaviours the same group) might have been sampled several times.

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

Group behaviours were defined as travelling (directed movement for longer than one minute at constant speed with flat surfacing), feeding (repeated steep surfacing and diving in different directions) and other (usually called "socialising" by other authors). Surface behaviours were spyhopping (vertical surfacing from the water, such that the head and eyes are exposed, diving back in the same position), leaping (jumps head first, such that at least three quarters of the body emerges from the water) and tailslapping (rising the tail out of the water and slapping on the surface).

As soon as killer whales were sighted one or several focal groups were chosen and the following information was noted for each focal group: date, location, number of animals in the three classes defined above, group behaviour, surface behaviours (including time and, if possible, class of individual showing the behaviour) and number of boats within 200 m of the whales.

It was not possible to conduct a multiple linear regression on the number of surface behaviours versus the explanatory variables because there were too many units with no observed surface behaviours. This would have meant a violation of the assumption of nor-

mally and homogeneously distributed residuals. Thus I conducted a logistic regression for each surface behaviour, modelling whether the behaviour occurred in a given unit by the duration of a unit, by the group size, by the group's behaviour, by the proportion of adult males and calves/juveniles, by the number of boats nearby, by cloud cover, by temperature and by wind speed. Additionally, the number of occurrences of each surface behaviour was modelled by the same variables using a Poisson regression (which assumes that the number of surface behaviours are Poisson distributed and can thus accommodate a large proportion of zeros).

Due to the small sample size, no interactions between explanatory variables could be included in the model. These could be of importance, e. g. when certain age–sex classes are more likely to perform a surface behaviour only during a specific group behaviour. Spyhops and leaps were observed in so few units that cloud cover, temperature and wind speed were omitted from their analyses. The two models for spyhops and leaps were mainly conducted to generate further hypotheses.

In a first step all explanatory variables were included in the logistic regression and then a stepwise backwards method was used to eliminate one non–significant explanatory variable at the time.

The statistical evaluation and the figures were done with S-plus, Version 3.2 on a Sun2 (e. g. Venables and Ripley, 1994). Residuals were checked graphically for a mean of zero and an absence of systematic variation with the predicted values.

Additionally, the time between occurrences of spyhops and tailslaps were compared with an exponential distribution using a Kolmogorov–Smirnov test (Siegel, 1987). An exponential distribution would be expected if the intervals between the occurrence of the behaviour were random (exponential distribution: $f(x) = 1 - e^{-\lambda x}$, $\lambda = 1/\text{average time difference}$).

Results

50 units could be observed for 2 to 83 (median 10) minutes. Groups consisted of 2 to 15 (median 5) individuals in total and were composed of up to 5 males and 3 calves/juveniles. The average number of boats per minute varied from 0 to 1, cloud cover from 0 to 8, temperature from –8 to 3 degrees Celsius and wind speed from 1.5 to 5.5 Beaufort.

Feeding was observed in 22, travelling in 27 and other behaviour in one unit(s). Tailslapping occurred up to 23, spyhopping up to 6 and leaping up to 15 times per unit and were observed 140, 15 and 21 times in total and during 22, 7 and 5 units, respectively.

The proportion of calves/juveniles and the duration of the observation of a unit were not predictive of whether tailslaps occurred during a unit. Tailslaps were more likely to be observed with increasing group size, during feeding and other behaviour (compared with travelling), with an increasing proportion of adult males, with decreasing number of boats, and with decreasing cloud cover, temperature and wind speed (Table 1 and Fig. 1).

The number of tailslaps per unit showed a similar dependency on the explanatory variables. The number of tailslaps also decreased with number of boats, temperature and wind speed. Instead of the duration of a unit, the size of the group increased the number of tailslaps that could be observed. Although a higher proportion of males leads to a higher probability that tailslaps occur, it leads to a decrease in the number of tailslaps shown. The inverse is true for cloud cover. Increasing cloud cover lowers the probability of occurrence of tailslaps but raises the number of tailslaps. Additionally, a higher proportion of juveniles leads to higher number of tailslaps (Table 2).

The probability of observing spyhops during a unit was not affected by the number of boats or by the proportion of calves/juveniles. It increased with the duration of the unit, with decreasing group size, while feeding (compared to travelling and other behaviour) and with de-

Table 1: The results of the logistic regression models for surface behaviours. For the non-significant variables the step number is given in which the variable became excluded.

| surface behaviour | TAILSLAPS | | SPYHOPS | | LEAPS | |
|-------------------------------------|--|-----------------------|---|-----------------------|--|-----------------------|
| | coefficients, variability | χ^2 , p-value | coefficients, variability | χ^2 , p-value | coefficients, variability | χ^2 , p-value |
| differences in log-likelihood | $\chi^2 = 46.259$, $df = 8$ p-value < 0.0001 | | $\chi^2 = 15.879$, $df = 5$ p-value = 0.007 | | $\chi^2 = 5.208$, $df = 1$ p-value = 0.022 | |
| Intercept | 2.737 12.448 | not tested | -0.599 12.404 | not tested | -4.471 1.307 | not tested |
| duration of unit ($df = 1$) | - | step 2 | 0.063 0.029 | 5.499 0.019 | - | step 5 |
| group size ($df = 1$) | 0.967 0.395 | 11.001 0.001 | -0.525 0.330 | 4.340 0.037 | 0.362 0.170 | 5.208 0.022 |
| group behaviour ($df = 2$) | - | 19.991 0.000 | - | 8.572 0.014 | - | step 3 |
| (1) feeding | 1.419 | - | 2.222 | - | - | |
| (2) other | 2.640 | - | -1.023 | - | - | |
| (3) travelling | -4.058 | - | -1.198 | - | - | |
| proportion of males ($df = 1$) | 7.406 4.014 | 5.415 0.020 | -3.755 2.172 | 4.060 0.044 | - | step 4 |
| prop. of juveniles | - | step 1 | - | step 2 | - | step 1 |
| number of boats ($df = 1$) | -9.288 3.866 | 9.003 0.003 | - | step 1 | - | step 2 |
| cloud cover ($df = 1$) | -0.879 0.471 | 5.197 0.023 | not included | | not included | |
| temperature ($df = 1$) | -0.746 0.364 | 5.988 0.014 | not included | | not included | |
| wind speed ($df = 1$) | -1.391 0.696 | 5.569 0.018 | not included | | not included | |

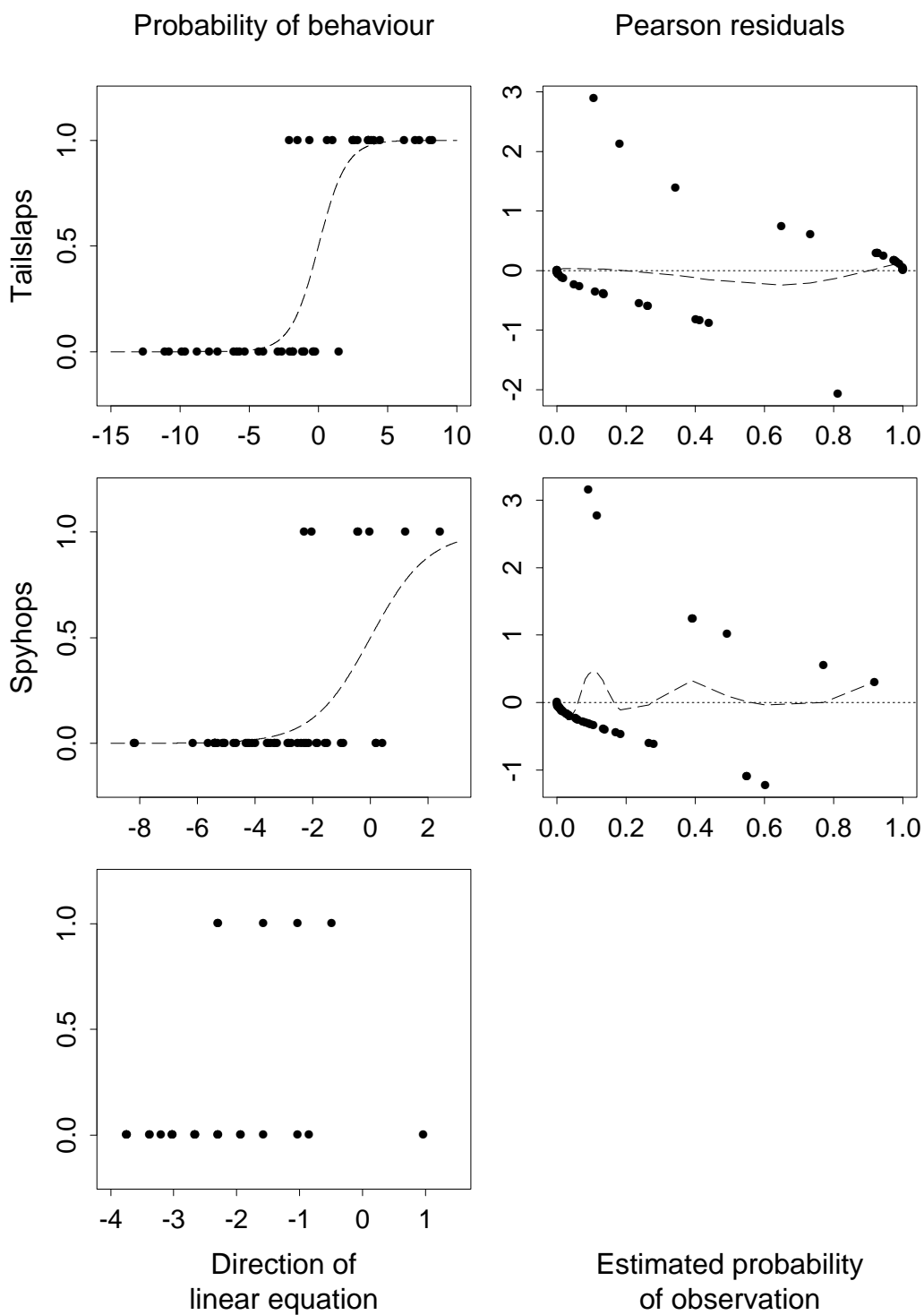


Table 2: The results of the Poisson regression models for the three surface behaviours.

| surface behaviour | TAILSLAPS | | SPYHOPS | | LEAPS | |
|-------------------------------------|---|-----------------------|--|-----------------------|--|-----------------------|
| | coefficients, variability | χ^2 , p-value | coefficients, variability | χ^2 , p-value | coefficients, variability | χ^2 , p-value |
| differences in log-likelihood | $\chi^2 = 237.701$, $df = 9$ p-value < 0.0001 | | $\chi^2 = 43.737$, $df = 5$ p-value < 0.0001 | | $\chi^2 = 93.628$, $df = 2$ p-value < 0.0001 | |
| Intercept | 2.722 0.531 | not tested | -1.499 10.008 | not tested | -0.533 0.301 | not tested |
| duration of unit ($df = 1$) | 0.018 0.007 | 6.739 0.009 | 0.046 0.014 | 11.473 0.001 | – | step 1 |
| group size ($df = 1$) | – | step 1 | -0.312 0.194 | 4.269 0.039 | – | step 5 |
| group behaviour ($df = 2$) | – – | 84.984 0.000 | – – | 12.968 0.002 | – – | 93.628 0.000 |
| (1) feeding | 1.241 | – | 2.236 | – | -1.172 | – |
| (2) other | -0.039 | – | -1.619 | – | 3.241 | – |
| (3) travelling | -1.202 | – | -0.617 | – | -2.070 | – |
| proportion of males ($df = 1$) | -1.227 0.490 | 7.224 0.007 | -3.889 1.644 | 9.254 0.002 | – | step 3 |
| prop. of juveniles ($df = 1$) | 10.160 1.817 | 35.225 0.000 | – | step 1 | – | step 2 |
| number of boats ($df = 1$) | -4.401 0.784 | 42.281 0.000 | – | step 2 | – | step 4 |
| cloud cover ($df = 1$) | 0.114 0.043 | 7.486 0.006 | not included | | not included | |
| temperature ($df = 1$) | -0.396 0.076 | 32.938 0.000 | not included | | not included | |
| wind speed ($df = 1$) | -1.053 0.181 | 69.753 0.000 | not included | | not included | |

creasing proportion of adult males (Table 1 and Fig. 1). The same pattern of dependency can be shown for the number of spyhops that occurred in a unit (Table 2).

The probability of observing leaps appears to depend only on group size. The non-significant variables that were excluded in the last two steps were the duration of the unit and the proportion of males (Table 1 and Fig. 1). The number of leaps seems only to depend on the behaviour shown. There were more leaps during other behaviour than during feeding and travelling. In this model the number of boats and group size were the second to last and last variable that were excluded (Table 2).

Neither the duration between tailslaps nor the duration between spyhops deviated from an expected exponential distribution (tailslaps: mean duration between tailslaps = 1.45 minutes, $\lambda = 0.689$, Kolmogoroff–Smirnov–test: $N = 21$, $D = 0.058$, $p > 0.2$; spyhops: mean duration between spyhops = 5.24 minutes, $\lambda = 0.191$, Kolmogoroff–Smirnov–test: $N = 21$, $D = 0.202$, $p > 0.2$).

53 adult males, 2 calves/juveniles and 12 females/subadult males were observed to perform tailslaps. This is proportional to the total number of animals observed in these classes ($\chi^2 = 2.525$, $df = 2$, $p = 0.28$). Only one male and two females could be sexed while spyhopping and only one juvenile recognised while leaping.

Discussion

Tailslaps occurred mainly during feeding (with some during “other” behaviour), with increasing group size and with an increasing proportion of adult males. This would support the hypothesis that tailslaps are used for stunning of prey while feeding on swarm fishes (Similä, 1997; Similä and Ugarte, 1993). But they may also have a social significance especially for adult males where they might be part of aggressive interactions (Slooten, 1994), even though the males only increased the probab-

ity of occurrence and not the number. The number of tailslaps increased with the proportion of young whales and it might be that the youngsters pick up the behavioural pattern from the adult males and try it out more often than is later necessary in social interactions.

Obviously, tailslaps also occur in orca populations from which no stunning of prey has been observed. Thus there might be a difference in function of surface behaviours between different populations (see also the introduction).

Tailslaps were also more likely to occur with decreasing number of boats and with decreasing cloud cover, temperature and wind speed. It is possible that boats disturb feeding behaviour close to the surface and that the orcas feed closer to the surface when weather conditions are more favourable. This might also be related to the fact that under favourable weather conditions, visibility is good close to the surface and in poor weather conditions, leapi e o

Neither tailslaps nor spyhops occurred in clusters. Thus a general social function of these behaviours is not supported. Either the occurrence of these behaviours is truly random or it is dependent upon so many variables that their sum is perceived as random.

At least for the use of tailslaps there is no indication of a differentiation among the age–sex classes. This behaviour is apparently not specifically used by one class for a special purpose (unless each class uses it for a different purpose).

No surface behaviour seemed to be caused by any one, single explanatory variable. Thus surface behaviours have several functions each, and/or the explanatory variables were sampled in too coarse a way.

If we want to learn more about the function(s) of surface behaviour it is crucial to be able to observe more details of the behavioural sequence of individuals (under water) in order to identify the exact context in which these behaviours occur. It might then become possible to assign functions to the surface behaviours even when they differ between contexts.

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