A survival guide to survival rates

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Introduction

The survival of marine mammals in captivity is often the subject of heated discussions. Interestingly, these discussions usually focus on cetaceans. The discussions are often complicated by a general lack of understanding of the subject matter. This can result in incorrect representation of the available data and comparisons of unrelated parameters. The terminology involved is not straightforward and can be confusing (Fad, 1996).
In this paper, I will discuss the terminology involved, the calculations that must be done to derive survival rates and life expectancies and I will look at the presentation of the data and how that can influence the message. A few examples will be given.

Some definitions

First, let's have a look at some of the terms. All these terms are derived from population dynamics modelling.

- *Daily Survival Rate* (**DSR**): the estimated proportion of animals alive on day *d* that is still alive on day *d+1* (DeMaster and Drevenak, 1988). The DSR can also be treated as a probability: then it is defined as the probability that an animal alive on day *d* will still be alive on day *d+1*.
- *Daily Mortality Rate* (**DMR**): This is the reverse of the DSR: it is the estimated proportion of animals alive on day *d* that will have died before day *d+1*.
- *Annual Survival Rate* (**ASR**): the estimated proportion of animals alive in year *t* that is still alive in year *t+1* (Olesiuk, *et al.*, 1990). The ASR can, like the DSR, also be treated as a probability: then it is defined as the probability that an animal alive in year *t* will still be alive in year *t+1*.
- *Annual Mortality Rate* (**AMR**): This is the reverse of the ASR: it is the estimated proportion of animals alive in year *t* that will have died before year *t+1*.
- *Life expectancy*: this is the average age a member of a certain population can be expected to reach. The life expectancy is a function of the ASR.
- *Longevity*: the maximum age a member of a certain population can reach. This is also sometimes called the maximum life expectancy.
- *Average age*: this is the average of all the ages of members of a population at a certain point in time (a "snapshot" of the population).
- *Animal days*:
    - For individual animals: the number of days between the time the animal first appeared in the population and either its death or the last day of the sample, if the animal is still alive.
    - For populations: the sum of the animal days for all the members of that population.
- *Animal years*: the same as animal days, but expressed in years instead of days.

Note that all these parameters are calculated for non-calf or non-pup animals (age > 1 year) (Small and DeMaster, 1995). The survival of calves and pups is incorporated in the calculation of reproductive rates. The focus of this paper is on survival rates. The reproductive parameters will be discussed only briefly.

Some background on reproductive rates

The following terms can be encountered in discussions about reproduction, as mentioned in [a]) Olesiuk *et al* (1990) and [b]) Wells and Scott (1990):

- *Fecundity rate* (**FEC**): This is the number of viable calves born per year as a percentage of the number of mature females or the proportion of mature females, giving birth to viable calves. [a,b]
- *Fertility rate* (**FER**): This is the total number of calves born per year as a percentage of the number of mature females or the proportion of mature females, giving birth [a]
- *Recruitment rate* (**REC**): This is the number of viable calves born per year as a percentage of the total number of animals in the population. [b]
- *Birth rate* (**BR**): This is the number of calves born per year as a percentage of the total number of animals in the population. [b]
- *Neonate mortality* (**MR_n**): This is the percentage of calves that die prematurely, i.e. before the age of 0.5 years [a] or before 1 year of age [a]. In the following I will use the one-year interval.

Mathematical background

In the following calculations, it is assumed that the ASR and DSR are independent of the actual age of the animals. This is probably not completely accurate. It is likely, that the survival rates differ for different age classes (Barlow and Boveng, 1991). However, the data available to date is insufficient to reliably determine age class dependent survival rates for most marine mammal species (due to a limited sample size) (Small and DeMaster, 1995).

The DSR can be calculated as follows (DeMaster and Drevenak, 1988):

$$DSR = 1 - \sum_{i=1}^{K} (y_i) / \sum_{i=1}^{K} (x_i)$$

where:

- K is the total number of animals in the sample
- y_i is 1 if animal i died during the reporting period and 0 if animal i is still alive at the end of the reporting period.
- x_i is the number animal days for animal i.

Or, in a simpler form (Small and DeMaster, 1995):

$$DSR = 1 - (\#deaths/\#animal\ days)$$

The annual survival rate ASR can be derived from the Daily Survival Rate DSR by raising the DSR to the power 365.25 (the average number of days in a year), as follows:

$$ASR = DSR^{365.25}$$

The annual mortality rate AMR is, by definition:

$$ASR = 1 - AMR$$

If we want to estimate the life expectancy for the population (the average number of years survived), we first need to calculate the total animal years. If we start out with N_0 animals, we need to know how many of them are left after one year, two years, etc. After one year, we have:

$$N_1 = s * N_0$$

In this and the following equations s is the ASR. After two years:

$$N_2 = s * N_1 = s^2 * N_0$$

And after *n* years:

$$N_n = s * N_{n-1} = s^2 * N_{n-2} = \ldots = s^n * N_0$$

If we add them all together, we get:

$$Total\ Years = N_0 + N_1 + \ldots + N_n = s^0 N_0 + s^1 N_0 + \ldots + s^n N_0$$

$$Total\ Years = \sum_{i=1}^{\infty} (s^i * N_0) = N_0 * \sum_{i=1}^{\infty} (s^i)$$

If we take infinitely small steps, we can rewrite this formula to:

$$Total\ Years = N_0 \int_0^{\infty} s^i\, di = N_0 \int_0^{\infty} e^{i*\ln(s)}\, di$$

This results in:

$$Total\ Years = N_0 \left. \frac{e^{i*\ln(s)}}{\ln(s)} \right|_0^{\infty} = N_0 \frac{e^{-\infty} - e^0}{\ln(s)} = \frac{-N_0}{\ln(s)}$$

To get the life expectancy, which is the average number of years, we need to divide the total number of years by the number of animals in the sample:

$$Life\ Exp. = \frac{Total\ Years}{N_0} = \frac{\left(\frac{-N_0}{\ln(s)}\right)}{N_0} = \frac{-1}{\ln(s)}$$

If we play around a bit with this formula, we can see that the life expectancy is very sensitive to errors. If there is only a small error in the estimate of the ASR, this can result in an error of several years in the derived estimate for the life expectancy. For that reason, life expectancy should not be used when comparing populations, captive or wild (DeMaster and Drevenak, 1988). See the table below for some survival rates, the corresponding life expectancies and the increase in both compared to the previous value in the table. You'll see that a 1% increase in survival rate results in a huge increase in life expectancy estimate for higher ASR values.

ASR	ASR increase	Life Expectancy	LE increase
0.920		11.99	
0.930	1.09 %	13.78	7.26 %
0.940	1.08 %	16.16	17.27 %
0.950	1.06 %	19.50	20.67 %
0.960	1.05 %	24.50	25.64 %
0.970	1.04 %	32.83	34.00 %
0.980	1.03 %	49.50	50.78 %

So far, we have not yet mentioned the longevity or maximum age. The reason for this is that there is no direct correlation between survival rate and longevity. Longevity is basically an incidental finding: it is determined by the oldest animal you find in your sample. You can only determine the longevity of a group of animals after all the members of that group have died (Duffield and Wells, 1991).

Sometimes, average age is used in comparing wild and captive populations (Duffield and Wells, 1991). The average age is calculated by adding the ages of all the animals in the population and dividing this by the number of animals. This is however of a very limited use. Such a comparison will only yield useful data if both populations have been stable for a long period of time (no increase or decline) (Barlow and Boveng, 1991). Only in a stable population, the calculation of the average age will yield the same result as the calculation of the life expectancy. If the size of a population is changing however, the average age can shift either way.

The reproductive rates

The neonate survival is the complement of neonate mortality:

$$SR_n = 1 - MR_n$$

From this we can calculate the relation between fecundity rate and fertility rate and between birth rate and recruitment rate:

$$FEC = FER * SR_n = FER * (1 - MR_n)$$

$$REC = FER * SR_n = FER * (1 - MR_n)$$

Where:

- SR_n is the neonate survival rate, the percentage of pups or calves surviving to the age of 1 year
- MR_n is the neonate mortality rate
- *FEC* is the fecundity rate
- *FER* is the fertility rate
- *REC* is the recruitment rate
- *BR* is the birth rate

Let's consider a declining population. There can be a number of reasons for the decline, such as:

- increase in mortality of older animals. In that case the number of (adult) animals dying will be higher than the number of calves being born into the population. As a result, the younger age classes will be over-represented and the average age will go down.
- decline in birth rate. In that case, an under-representation of the younger age classes can be expected and the average will increase, as has been noted in the Alaskan Northern sea lion population (York, 1994).

Also increases in population size can shift the average age either way:

- if the increase is caused by an increase in birth rate, the population will have an increasing number of young animals and consequently, the average age will go down.
- if the increase is caused by a reduction in mortality, more older animals will remain in the population and the average age will go up.

So, a higher average age does not necessarily mean that a certain population is doing better than another population with a lower average age.

Presenting the data

Now let's look at some numbers. Consider a population with an annual survival rate of 0.95 (this value is in the same range as the survival rates for a number of marine mammals (see below)). All the following statements are correct, but the impact of the message can be quite different.

1. The annual survival rate is 95%
2. The annual mortality rate is 5%.
3. The life expectancy is 19.5 years.
4. The majority of the animals will become older than 13 years.
5. Within 5 years, 23% of the animals will have died.
6. One third of the animals survives no longer than 8 years.
7. Within 14 years 50% of the animals will be dead.

Statements 1 and 2 are fairly neutral and "scientifically correct". If you want to paint a positive picture, you will use statements like 3 and 4, whereas statements 5 through 7 have a negative ring to them. To paraphrase an old song: "t Aint what you say, it's the way that you say it"

Some real numbers

Now that we know how we can calculate the numbers and how we can present them, let's look at some published data that is available for wild and captive populations. There have been 2 detailed studies done on captive populations, one dealing with all the data available until the time of publication (covering captivity data from 1940 to 1985 (DeMaster and Drevenak, 1988)) and a more recent one, evaluating the previous study and concentrating on the data from 1988 to 1992 (Small and DeMaster, 1995). Both studies took the data from the MMIR (Marine Mammal Inventory Report), maintained by the National Marine Fisheries Service. The MMIR has been shown to be quite accurate (Temte, 1993):

> "*Overall, the Marine Mammal Inventory Report is an excellent source of highly accurate, unbiased, and complete data on census, status, and selected biological processes of marine mammals in captivity*."

There have been some studies done on wild populations of a few species of marine mammals. Of the species, covered in studies of captive marine mammals (DeMaster and Drevenak, 1988, Small and DeMaster, 1995), comparative studies of wild populations are available for:

- the bottlenose dolphin (*Tursiops truncatus*): the Sarasota population (Wells and Scott, 1990) and the Indian Banana river population (Hersh, et al., 1990)
- the killer whale (*Orcinus orca*): the Washington and British Columbia population (Olesiuk, et al., 1990)
- the Steller sea lion (*Eumetopias jubatus*): the Alaska population (York, 1994)

Species	**Population**	**Annual Survival Rate**
Bottlenose dolphin	Sarasota, Florida[1]	0.961
	Indian/Banana River, Florida[2]	0.920
	oceanaria (1940-1985)[3]	0.930
	oceanaria (1988-1992)[4]	0.951
Killer whale	British Columbia and Washington[5]	0.976
	oceanaria (1940-1985)[3]	0.930
	oceanaria (1988-1992)[4]	0.937
Beluga	oceanaria (1940-1985)[3]	0.940
	oceanaria (1988-1992)[4]	0.954
Steller sea lion	Alaska[6]	< 0.930
	oceanaria (1940-1985)[3]	0.964
	oceanaria (1988-1992)[4]	0.969
California sea lion	oceanaria (1940-1985)[3]	0.935
	oceanaria (1988-1992)[4]	0.952

1. Wells and Scott, 1990
2. Hersh, et al., 1990
3. DeMaster and Drevenak, 1988
4. Small and DeMaster, 1995
5. Olesiuk, et al., 1990
6. York, 1994

For bottlenose dolphins, the difference between the survival rates in captivity (both the whole period 1940-1992 and the subset 1988-1992) and the Sarasota population is not statistically significant. The survival rates for killer whales in captivity are lower than in the wild, whereas the survival rates for Steller sea lions are significantly higher in captivity than in the wild. For the California sea lion and the beluga, no data are available on the survival rates in wild populations.

There is little information about the reproductive rates and calf mortalities in wild cetaceans. Wells and Scott (1990), for the Sarasota population of bottlenose dolphins, calculated a maximum survival rate to age 1 of 0.811 (an average ASR to age 1 of 0.803). Olesiuk et al (1990) estimated the calf mortality in killer whales at 43%. Since they calculated calf mortalities as mortalities up to 0.5 years, this means a survival rate to age 0.5 of 0.57. Assuming a survival rate between age 0.5 and 1 comparable to adult whales (0.976), the ASR to age 1 could be 0.563. Small and DeMaster (1995) report calf/pup survival rates for the captive population (through December 1992) of 0.666 for bottlenose dolphins and 0.858 for California sea lions.

An example: The survival rate of the Särkänniemi dolphins

Calculation of the survival rates for a known population is pretty straightforward. As an example, let's have a look at the dolphins in the Särkänniemi Delfinaario in Tampere, Finland. Five dolphins arrived at the facility on March 31st, 1985, so their first full day at the facility was April 1st, 1985. We will consider the period April1st, 1985 until June 12th, 2000 for this calculation. To be able to calculate the survival rate, we need to calculate the total number of animal days for that period. At the end of the sampling interval, 4 of the 5 original dolphins were still alive. One of the males, Joona, died on September 7th, 1990. During the sampling period, two calves were born that survived beyond one year of age. On August 18th, 1993 a male calf named Leevi was born and on September 9th, 1996, another male calf, Eevertti, was born. Both were still alive at the end of the sampling period. The days collected for Leevi and Eevertti since their first birthdays (August 18th, 1994 and September 9th, 1997) must also be included. So this leads us to the following data:

Name	Start date	End date	Animal days
Niki	01-04-1985	12-06-2000	5551
Näsi	01-04-1985	12-06-2000	5551
Veera	01-04-1985	12-06-2000	5551
Joona	01-04-1985	07-09-1990	1985
Delfi	01-04-1985	12-06-2000	5551
Leevi	18-08-1994	12-06-2000	2125
Eevertti	09-09-1997	12-06-2000	1007
Total			27321

Now that we have calculated the total number of animal days, we can calculate the Daily and the Annual Survival Rates for this group:

$$DSR = 1 - (\#deaths/\#animal\,days) = 1 - (1/27321) = 0.9999634$$

$$ASR = DSR^{365.25} = 0.9999634^{365.25} = 0.98672$$

So, based on the data collected so far, the ASR for the Särkänniemi dolphins is calculated to be approximately 0.986 (95% confidence interval: 0.961-1).

Average longevity vs. survival rates

In online discussions on the BBC Animal Zone web site and on the alt.animals.dolphins newsgroup, some people claimed that the life expectancy of dolphins in captivity was only 5.3 years. Apparently, that number came from William Johnson's book "The Rose-tinted menagerie" (1990). In chapter 4.1, Johnson states:

> "*According to statistics provided by the UN's Food and Agricultural Organisation (FAO), dolphins in the wild can live up to 30 years, but their average life expectancy in captivity is a mere 5.3 years.* "

However, this is a serious misquote of the original report. It illustrates a lack of understanding of the subject matter, which is not uncommon in discussions about survival. To clarify the issue, let's examine the original FAO paper (Cornell and Asper, 1981) This paper does not deal with life expectancy, but with average longevity up to 1976. This has virtually no relationship with life expectancy. Basically what the authors did is tally up the time survived in captivity up to 1976. They added the life span of animals that were dead before that date (real longevity of those animals) and the ages of animals in captivity that were still alive at the time. So an animal born in 1975 would count for one year only, even though that particular animal might even be alive today, in which case its longevity would exceed 24 years.

Part of the aim of the paper was to compare numbers of animals brought or born into captivity prior to the Marine Mammal Protection Act (MMPA) and the so-called post-MMPA animals. A direct quote from the paper:

> "*Less than four years have passed since the implementation of the Act, therefore the maximum longevity of animals collected after the Act would be 3 years and 8 months. Most post-Act animals have not been in captivity for so long, and many have only been recently acquired*".

The method of calculating life expectancies (or actually survival rates, from which life expectancies can be derived) is quite different from the methods used in the FAO paper and comparing the numbers from this paper to life expectancies from other papers is invalid.

DeMaster and Drevenak (1988) say, with respect to the average number of days survived in captivity (which is the same as the average longevity mentioned above):

> "*However, these statistics are of no real use in evaluating the husbandry record of the public display industry unless the entire cohort of animals that are used in estimating this statistic is dead. When this is not the case, this method of calculating longevity is very sensitive to the proportion of animals that have been recently acquired. In this study most of the animals included in the marine mammal inventory were not dead. Because some animals have survived in captivity for over 30 yr, it is not possible to do a meaningful analysis of the data at this time with this statistic because of the limited number of animals that could be used in the analysis*".

To show the difference between the methods consider the following hypothetical case:

- on day 0, 10 animals are acquired
- two years later (on day 730) one of the animals dies which leaves 9 animals alive.
- at that same date we take our sample, so we have 10 animals which have lived 2 years up to the sample date. The average longevity is then 2 years. (This is the method used in the FAO paper).
- For the calculation of survival rates, we have collected 7300 animal days and we have recorded 1 death. This leads to a daily survival rate of 0.99986 or an annual survival rate of 0.951. This translates to a life expectancy for this "population" of 19.98 years. (This is the method used by Wells and Scott (1990) and Small and DeMaster (1995) to calculate survival rates for the wild and captive populations).

To demonstrate the difference between the methods even further, lets vary the number of deaths occurring on day 730:

Nr of deaths	Average longevity	Survival rate	Life expectancy
0	2 yrs	undetermined	undetermined
1	2 yrs	0.951	19.98 yrs
2	2 yrs	0.904	9.99 yrs
3	2 yrs	0.861	6.66 yrs
4	2 yrs	0.819	5.00 yrs
5	2 yrs	0.779	4.00 yrs
6	2 yrs	0.740	3.33 yrs
7	2 yrs	0.704	2.85 yrs
8	2 yrs	0.670	2.50 yrs
9	2 yrs	0.637	2.22 yrs
10	2 yrs	0.606	2.00 yrs

As you can see, the number of deaths has no influence on the average longevity in this case. The number remains the same, no matter how many deaths occurred. However, the survival rate and the derived life expectancy go down drastically if more deaths occur. Only when all animals in the sample are dead at the end of the sample period do the average longevity and survival rate yield match.

In short, the average longevity and the life expectancy are vastly different. They cannot and should not be compared. If you want to compare the captive population with wild populations, always check the original references to make sure you compare the same parameters.

Conclusion

Now that we have examined the terminology involved and have seen some published data, let's examine some examples of flawed or incomplete representations, both from anti-captivity organizations and from the captive display industry.

- *The average life span of a dolphin in the wild is 45 years; yet half of all captured dolphins die within their first two years of captivity. The survivors last an average of only 5 years in captivity.* (Dolphin Project Europe, 1996)
  This is incorrect. 45 years is the (maximum) longevity for dolphins in the wild, not the average life span (life expectancy) (Wells and Scott, 1990). The same study showed that the Annual Survival Rate for the Sarasota population was 0.961, which translates to a life expectancy of about 25 years. Small and DeMaster (1995) calculated an ASR for the captive population of 0.951, which translates to a life expectancy of 19.9 years. If the life expectancy in captivity would be only 5 years, the associated ASR would be 0.819, which is not even close to the measured value.
- *At least 134 orcas (killer whales) have been taken into captivity from the wild since 1961. One hundred and three (77%) are now dead* (WDCS, 1999)
  While this information may be correct, no conclusions can be derived from this since no timing details are given which would allow the calculation of animal days or years.
- *Of the 103 which died, average length of survival in captivity was under six years (range: 1 day - 27.2 years)* (WDCS, 1999)
  Selecting data on animals based on the fact that they are dead introduces a bias towards the shorter lived individuals. The ones that are doing better and are still alive are excluded from the statistics.
- *Of 54 known pregnancies in captivity since 1968, only 21 calves (39%) have survived.* (WDCS, 1999)
  This seems to suggest that calf survival in captivity is low. While a 39% survival rate may seem low, it is in the same order of magnitude as wild calf survival, estimated by Olesiuk et al (1990) at 43% for the BC population.
- *Another indicator that dolphins are living as long in zoological collections as in the world is research by Drs. Deborah Duffield of Portland State University and Randall Wells of the Chicago Zoological Society. Their data show that the average age of dolphins in their natural environment is similar to that of dolphins in public display facilities. This work corroborates a study published in 1988 by DeMaster and Drevenak (Marine Mammal Science, 4:297-311, 1988) which pointed out that survival of dolphins in aquariums "may be better than or equal to survival in the wild."* (Dolphin Quest, 1999)
  The Duffield and Wells (1991) study quoted uses average age of animals as an indicator. As pointed out earlier, this is not a reliable measure, unless the populations have been stable for a long period of time. This is uncertain for the Sarasota population and not true for the captive population. In addition, the quote from DeMaster and Drevenak (1988) is incorrect. Actually, they noted: "*<...> At this time it is not possible to compare survivability of animals in captivity with that of animals in the wild.<...> Additional data from free-ranging animals are needed to determine if captive animals have similar life expectancies.*"

- *The average life expectancy for bottlenose dolphins in their natural environment in the best studied population is 7.0 years for females and 10.1 years for males. The average age at death for captive bottlenose dolphins over the last 20 years has been 11.1 years for females and 10.9 years for males.* (Minnesota Zoo, 1999)
  This is an incorrect quote from the Duffield and Wells (1991) paper. The numbers quoted are the average ages at death recorded, not life expectancies (the paper does not mention life expectancies). Also the numbers involved are low: the age at death for wild females was based on only one animal (the only confirmed female death).

Hints and tips

When you get involved in discussions about marine mammal survival, keep the following things in mind:

- look out for false comparisons (like comparing longevity with life expectancy)
- stay away from life expectancy estimates: use survival rates instead.
- verify claims about life expectancies and survival times by converting them to survival rates.
- know and verify the published data about this subject.
- look for proper reasoning in your own statements and those of others. A useful tool for this is the Baloney Detection Kit (Sagan, 1996; online at: http://www1.tpgi.com.au/users/tps-seti/baloney.html).

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Appendix: Confidence Intervals

Confidence intervals for the DSR can be calculated from a binomial distribution, where the binomial parameter is set to (1-DSR) or DMR. Drevenak and DeMaster (1988) used a method of interpolation to get the confidence intervals. However, the confidence interval can be calculated from the Standard Error (SE), which can be calculated directly. The Standard Error for a binomial distribution (as a proportion rather than absolute numbers) can be calculated as:

$$SE = \sqrt{\frac{p * q}{k}} = \sqrt{\frac{p * (1 - p)}{k}}$$

Substituting the standard parameters with the variables we use in the DSR calculations we get:

$$SE = \sqrt{\frac{DSR * DMR}{\#animal\,days}}$$

The confidence interval is then defined as:

$$(DSR - 1.96 * SE) \leq \mu \leq (DSR + 1.96 * SE)$$

where represents the real value of the DSR.

For more information see:

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Paper history

This paper has been presented at:

- the 24th Annual Conference of the International Marine Animal Trainers Association, November 5-8, 1996, Gold Coast, Australia.
- the 25th Annual Symposium of the European Association for Aquatic Mammals, March 14-17, 1997, Duisburg, Germany

A formal version has been published in:
Marine Mammals: Public Display and Research **3(1)**: 27-38.

This version has been created on June 12, 2000. Main differences with the conference and paper versions are:

- Updated the Särkänniemi data, reflecting the situation on June 12, 2000
- Added information about reproductive rates
- Added a chapter on average longevity vs. survival rates
- Updated examples in the Conclusion section to included references from both the anti-captivity movements and the captive display industry
- Added information about confidence intervals added as an appendix