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THE CONSTITUTIONAL BASIS OF LONGEVITY IN THE CETACEA: DO THE WHALES AND THE TERRESTRIAL MAMMALS OBEY THE SAME LAWS?

by

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ABSTRACT

The maximum lifespans in captivity for terrestrial mammalian species can be estimated by means of a multiple linear regression of logarithm of lifespan (*L*) on the logarithm of adult brain weight (*E*) and body weight (*S*). This paper describes the application of regression formulas based on data from terrestrial mammals to the estimation of odontocete and mysticete lifespans. The regression formulas predict cetacean lifespans that are in accord with the data on maximum cetacean lifespans obtained in recent years by objective age determination procedures. More remarkable is the correct prediction by the regression formulas that the odontocete species have nearly constant lifespans, almost independent of body weight over a 300:1 body weight range. This prediction is a consequence of the fact, remarkable in itself, that over this body weight range the Odontoceti have a brain:body allometric slope of 1/3, as compared to a slope of 2/3 for the Mammalia as a whole.

INTRODUCTION

The biology of longevity is a two-sided problem. On the one hand, there is the problem of determining the ages of animals in the wild, and of using such data to construct valid life tables and reproductive histories. This problem is being studied actively in the odontocete whales, as this conference attests, and also in a number of other vertebrate species.

The other side of the biology of longevity is concerned with identifying the evolutionary, ecological, and molecular-cellular factors that contribute to the determination of animal lifespans and life tables. This too is an active field, especially in those aspects that are of interest in theoretical population biology, but it does not receive the attention that it merits in the aspect that I shall discuss here, the relation of species longevity to constitutional factors such as body weight and length, organ weights, energy metabolism, and reproductive factors.

I shall briefly review the conclusions about the constitutional basis of longevity that have been educed from the study of longevity in the terrestrial mammals, and apply these to the estimation of the lifespans of cetacean species. The discussion will show that despite the great disparity in their environmental adaptations and body dimensions, the whales and the terrestrial mammals have a consistent quantitative relation of longevity to brain and body size.

CONSTITUTIONAL CORRELATES OF LIFESPAN IN TERRESTRIAL MAMMALS

The investigation of the relation of mammalian lifespan to constitutional characteristics goes back to the work of Rubner (1908) on the relation of lifespan to body weight and metabolic rate, and to the work of Friedenthal (1910) on the relation of lifespan to brain weight. I took up this problem again in the 1950's, when it became evident that we need quantitative data about these relationships if we are to understand the evolution of longevity in vertebrates.

In my previous work on terrestrial mammals, the lifespan statistic used was the maximum lifespan recorded for the species under conditions of captivity. In view of the unique characteristics of zoo longevity data (Sacher, 1979), the maximum lifespan is a better estimate of the species longevity parameter than the life expectation, because the life expectation is more influenced by environmental factors than is the maximum lifespan, and because valid life expectations could not be calculated from the heterogeneous and unevenly reported longevity data gathered from zoos throughout the world.

My first analysis of longevity in terrestrial mammals was based on a sample of 67 species for which lifespan, brain weight, and body weight were tabulated (Sacher, 1959). Subsequently I compiled a series of 239 species for which these three variables were measured, and it is some of the statistics from this latter sample that I shall discuss here (Sacher, 1976, 1978). The relations of lifespan, L, to brain weight, E, and body weight, S, are allometric in that the relations of the logarithms of these variables are linear. Lifespan is influenced independently by brain weight and body weight but these two variables are intercorrelated, so that it was necessary to calculate the multivariate regression of logarithm of lifespan on the logarithms of brain weight and body weight. The least squares relation, from the sample of 239 species was found to be

$$\log L = 0.519 \log E - 0.173 \log S + 0.982. \tag{1}$$

The standard error of estimate is 0.138, corresponding to a percentage error of ± 37%. The 239 species in this analysis were drawn from 12 orders of terrestrial mammals, with the bats excluded.

Several major taxa, including the orders Rodentia and Artiodactyla, and the suborder Anthropoidea, had a sufficiently large number of representatives in the sample so that the multivariate regressions could be calculated for these taxa individually. The relation for the Anthropoidea is particularly interesting here, because this group is comparable to the cetaceans in degree of cephalization and in lifespan. The regression for the Anthropoidea was found to be

$$\log L = 0.684 \log E - 0.202 \log S + 0.871. \qquad (2)$$

This was based on a sample of 43 species, and the standard error of estimate was 0.111, corresponding to a percentage error of ±29%. The relations for the orders Rodentia and Artiodactyla were not significantly different from the relation found for the Anthropoidea (Sacher, 1975).

Another way of examining the dependence of lifespan on brain and body weight for the mammals is to average the logarithms of these variables for each of the 12 orders and then to do a regression based on the averages for orders. This yielded the regression relation

$$\log L = 0.655 \log E - 0.244 \log S + 1.047. \qquad (3)$$

This equation, based on a sample of 12 terrestrial orders, again excluding bats, has a standard error of estimate of 0.060, corresponding to a percentage error of ±15%, and does not differ significantly from the relation for the Anthropoidea (Eq. 2) (Sacher, unpublished).

These regression relations show that there is a single relation of longevity to brain and body weight between and within orders of terrestrial mammals, although some residual inhomogeneity remains to be accounted for. However, the negative coefficient of partial regression of lifespan on body weight was somewhat puzzling, for the high negative correlation between body weight and metabolic rate would lead one to expect a positive relation of lifespan to body weight. To examine this question further I drew another sample of 85 species for which, in addition to brain and body weight, there were also data on the resting specific metabolic rate, M, in calories per gram, and for the body temperature, T_b. The regression of lifespan on these four variables was

$$\log L = 0.62 \log E - 0.41 \log S - 0.52 \log M + 0.026 T_b + 0.90. \qquad (4)$$

The partial regression on body weight, S, is now more negative than in the previous three equations, but there is also a negative dependence on log metabolic rate of -0.52. This negative dependence of lifespan on metabolic rate is in accord with the theoretical expectation, while the negative dependence of lifespan on body weight indicates that there is another contribution of body weight to longevity, independent of the relation of body weight to metabolic rate, possibly arising from the relation of body weight to brain weight. These matters have been discussed elsewhere (Sacher, 1978).

RESULTS

Table 1 gives data on adult brain weights and body weights of a number of odontocete and mysticete whales. Also given in Table 1 are the observed maximum lifespans, obtained by objective age determination procedures, such as dentrine or cementum growth layers in the odontocetes and ear plug layer counts in the mysticetes. The two right-hand columns of Table 1 give maximum lifespan estimates obtained from the regression of log lifespan on log brain weight and log body weight for terrestrial mammals. Two estimates are given, using Eqs. 1 and 3.

Figure 1 gives a plot of brain weight against body weight for odontocete species, on logarithmic scales. Several species are plotted that are not tabulated in Table 1. A straight line is drawn through the points with a predetermined slope of 1/3.

Data on the metabolic rates and body temperatures of several cetacean species are reviewed by Lockyer (1976a, b), but such data are available only for *Physeter* and *Tursiops* among the odontocetes, and the additional information on metabolic rate and body temperature does not improve the lifespan estimates for these species. This is not an unexpected outcome, and the situation can be expected to improve as better data become available.

DISCUSSION

The two-variable relationship based on 239 terrestrial species (Eq. 1) yields predicted lifespans that are in fairly good agreement with the observed values for the odontocetes, but tend to be lower than the observed values for the mysticetes. The lifespan estimates given by Eq. 3 are higher than the estimates from Eq. 1 for the odontocete species, and approximately equal to the estimates from Eq. 1 for the mysticete species. The two regression relations utilize the same data, but in somewhat different ways. I believe that Eq. 3 gives a somewhat better estimate of cetacean lifespans than does Eq. 1, for reasons given elsewhere (Sacher, 1978)*.

It should be borne in mind that these equations predict the lifespans that would be observed for these species in captivity, if captive conditions were as benign for the whales as they are for most terrestrial species. Therefore we should expect the predicted maximum spans to be somewhat above the maximum observed lifespan values for the free-living animals. This expectation is confirmed for the odontocetes, but not for the mysticetes. A possible reason for the low lifespan estimates for mysticetes is discussed below.

The relation of lifespan to the constitutional variables for the odontocetes has some remarkable features. The first of these may be seen in Fig. 1, in which brain weight is plotted against body weight on a log-log grid. The data points, especially above 100 kg body weight, lie along a line with slope of about 1/3. The line through the points is drawn with slope 1/3, not as a best fit, but rather with the intention of showing that the data have approximately this slope. The 1/3 slope does not apply to the species with body weights below 100 kg, and in this region the points follow a somewhat steeper slope, which is, however, not too well defined because the body weight range is short relative to the scatter around the line.

This well defined 1/3 slope for the odontocetes is unique: The allometric brain:body slope for the mammals as a whole is 2/3 (Sacher, 1976). No other mammalian taxon above family rank has a brain:body relation of comparablly low slope, and in the families or subfamilies for which such a low-slope relation is observed, the body weight range is much narrower, at most a 10:1 range, as against the 300:1 range for the odontocete species with body weights above 100 kg.

Returning to Eq. 1, let us set lifespan, L, equal to some constant value, L^*, and solve for the relation of E to S when lifespan is held constant. This relation is

$$\log E = 0.33 \log S + 1.93 \log L^* - 1.89. \qquad (5)$$

In other words, the data for terrestrial mammals contain the implication that all species with brain weights and body weights lying along a straight line with slope of about 1/3 should have the same lifespan.

The implication of the 1/3 power brain:body relation for the odontocetes is, therefore, that those species with body weights above 100 kg should have constant lifespans, independent of body weight. Inspection of Table 1 reveals that odontocete lifespans have only a narrow range of variation, and, moreover, do not have a significant correlation with body weight over the 300:1 range of body weights.

The inference that lifespan is constant along a 1/3 power brain:body trend line was established from data on terrestrial mammals, yet there is no terrestrial taxon that exemplifies this relation as clearly as do the odontocetes. The family Ursidae (bears) and the subfamily Mustelinae (weasels) are the terrestrial groups that most clearly display approximately 1/3 power brain:body allometry (Sacher, unpublished), but the narrow range of body weights in the case of the Ursidae, and the paucity of longevity data in the case of Mustelinae, preclude any conclusive test of the hypothesis that lifespan in these groups is constant, independent of body weight.

The next question is, of course, "Why do all odontocete species have almost constant lifespans?" The definitive answer lies in the future, but the fact that this near-constancy was predicted by a brain:body relation educed from the terrestrial mammals means that the explanation, when it is found, must be valid for the Mammalia as a whole, and not merely for the Odontoceti.

Some of the difficulties and uncertainties of the regression estimates of cetacean lifespans need to be considered. One question is how to take account of the differences in body composition between most terrestrial mammals and the larger cetaceans. The proportion of body fat is considerably greater in the mysticetes than in any land mammal. One solution to this problem is to use body length instead of body weight. Body length is a better size variable than is body weight on theoretical grounds, and there is the practical advantage that voluminous data on body length are available for cetacean species, but very few good body weight determinations.

Further evidence is needed on the question whether the metabolic rates of the odontocetes and the mysticetes are systematically higher or lower than those of the typical terrestrial mammals. The discrepancies between observed and estimated lifespans for the mysticetes, in which the predicted values are lower than those calculated from ear plug layer counts, may be a result of the combined errors arising from the large blubber mass and from a lower mysticete metabolic rate than would be expected from the Brody-Kleiber relation for the terrestrial mammals (Kleiber, 1947).

There are no useful longevity records for cetaceans in captivity, so it will be necessary to develop a new basis for cetacean longevity analysis. The choices are:

a) Maximum age in harvested samples, determined by age-determination procedures such as tooth layers or by marking and recapture;

b) Mean annual natural mortality rate or its reciprocal, mean survival time.

Method (a) is used here because it is most consistent with the maximum longevity datum used for the analysis of data from terrestrial mammals. The theoretical basis is weaker, however, because the mortality processes of free-living cetacean (and terrestrial mammal) populations are dominated by the age-independent mortality arising from environmental causes, and in these circumstances the oldest age in the sample is not in general a good estimate of the real longevity limit for the species set by its underlying, but unexpressed, Gompertzian mortality process (Sacher, 1959). Nevertheless, the maximum age does give information about the attainable species longevity, especially if, as in the present instance, the samples for all species are reasonably large and comparable in size, on the order of hundreds of animals.

In the long run, the phylogenetic analysis of mammalian longevity must be reexamined using annual mortality rate or a comparable measure of the age-independent mortality term, not because it is a "better" statistic, but rather because it is a different statistic which measures the ecologically imposed limits on survival, whereas maximum lifespan, when properly determined, estimates the intrinsic limits on longevity set by the senescence process.

These two mortality terms are functionally related across species as a consequence of selection for fitness, so a major agenda item for the ecological gerontology of the future will be working out the nature of that relationship. Considerations such as those presented above may provide the basis for understanding the remarkably uniform species lifespans over the great size range of the toothed whales.

CONCLUSION

Two remarkable inferences have emerged from this analysis of the relation of lifespan to brain weight and body weight in the Cetacea. First, the relations between these variables educed from data on terrestrial mammals are found to be in good agreement with the cetacean data, which strengthens the conclusion that there is a single relation among these three variables for all homeothermic mammals.

The second striking finding is that the brain:body allometric relation for the odontocetes has a low slope of approximately 1/3 and that this relation, when inserted into the longevity regression relation for the terrestrial mammals, made a correct prediction that odontocetes have nearly constant lifespans, independent of body weight.

The near-constancy of the maximum lifespans of odontocetes, and its coupling with the unique 1/3 slope of their brain:body allometry, is an intensely interesting finding, which needs to be examined more thoroughly, for these relationships imply that there is an ecological or physiological constraint on the population biology of the Odontoceti.

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Table 1

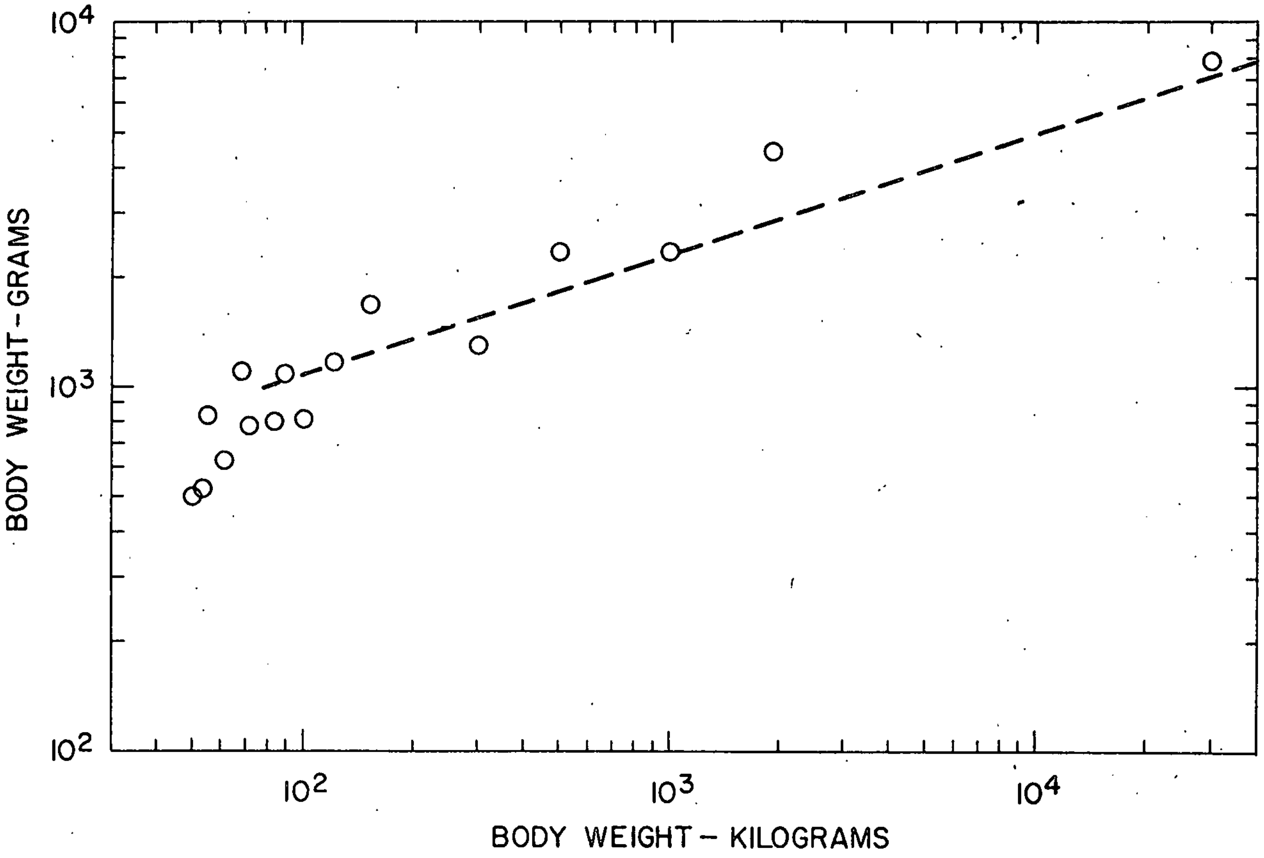
Brain weights, body weights, and observed and predicted lifespans for cetaceans. Estimates are from two-variable regression formulas based on terrestrial mammals, Equations 1 and 3 in the text. The references are for the maximum measured lifespans.

	Brain wt. g E	Body wt. g x 10^{-6} S	Reference	Lifespan, years		
				Observed	Predicted Eq. 1	Predicted Eq. 3
		ODONTOCETI				
Berardius bairdii	--	--	1	71		
Delphinapterus leucas	2350	0.45	2	40	66	75
Delphinus delphis	829	0.085			51	57
Globicephala melaena	2450	0.85	3	56	60	66
Hyperoodon ampullatus	2780		4	37		
Lagenorhynchus acutus	1200	0.120			58	67
Lagenorhynchus obliquidens	1140	0.090			60	69
Orcinus orca	4500	1.86			72	81
Phocaena dalli	834	0.098			50	55
Phocaena phocoena	515	0.053			43	47
Physeter catodon	7875	30	5	49	60	60
Stenella attenuata ♀			6	46		
Stenella coeruleoalba ♂♀			7	58		
Stenella graffmanni	780	0.077			50	56
Stenella styx	855	0.055			56	65
Tursiops truncatus	1690	0.15			67	79
		MYSTICETI				
Balaena mysticetus	5900		8	>40		
Balaenoptera borealis	4460	50	9	70	41	36
Balaenoptera physalus	6820	59	10	>50	49	46
Megaptera nodosa	6250	40	8	>29	50	48
Sibbaldus musculus	6610	75		--	47	42

1. Kasuya, 1977.
2. Khuzin, cited by Brodie, 1971.
3. Kasuya, personal communication; Sergeant, 1962.
4. Christensen, 1973.
5. Gaskin and Cawthorn, 1973.
6. Kasuya, 1976.
7. Kasuya, 1978, and personal communication.
8. Slijper, 1961.
9. Lockyer, 1974.
10. Nishiwaki et al., 1958.

FIGURE LEGEND

Figure 1. Relation of brain weight to body weight for the odontocetes. Each point represents a different species. Data plotted on logarithmic scales. The straight line has assigned slope of 1/3, and is drawn near the data points to show how closely the data for species weighing more than 100 kg follow a slope of 1/3.


10^4
10^3
10^2
BODY WEIGHT - GRAMS
10^2
10^3
10^4
BODY WEIGHT - KILOGRAMS