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Species differences in decompression

T. E. BERGHAGE, T. D. DAVID, and C. V. DYSON

Behavioral Sciences Department, Naval Medical Research Institute, National Naval Medical Center, Bethesda, MD 20014, USA

Berghage, T. E., T. D. David, and C. V. Dyson. 1979. Species differences in decompression. Undersea Biomed. Res. 6(1): 1–13.—In an effort to bring together the diverse laboratory-animal decompression studies, a literature review and statistical evaluation were undertaken. Although 22 different species that had been used in decompression studies were identified, systematic data were available for only 7 of these species: man, goat, dog, guinea pig, rat, hamster, and mouse. Mathematical functions using physiological data on these seven species were developed to estimate 1) saturation time (the time for the body to equilibrate after an increase in hydrostatic pressure), and 2) no-decompression saturation-exposure limits (the maximum saturation-exposure pressure from which an abrupt return to 1 ATA can be tolerated). Data from man, rat, and mouse were used to develop physiological relationships for two additional decompression variables: change in pressure-reduction limits associated with increased exposure pressure and time to onset of decompression symptoms. Finally, data on rats for two other decompression variables, gas elimination time and optimum decompression stop time, are discussed in the hope that this will stimulate additional animal laboratory research in other mammalians. The general functional relationships developed in this paper provide a preliminary and rough means for extrapolating among species the decompression results obtained during animal laboratory experiments.

animal
decompression
decompression theory

When Robert Boyle decompressed a snake in a vacuum chamber in 1670 and observed a bubble in its eye, he unknowingly inaugurated the study of decompression phenomena. Before this time it had been physically impossible to reduce ambient pressure fast enough to produce emboli. Boyle's observation remained an isolated laboratory phenomenon until the mid 1800's. At that time the air-compression technology of the French scientist Freminet was coupled with the caisson technology of Triger to produce a system that allowed men to work for several hours under increased hydrostatic pressure. These prolonged stays in the hyperbaric environment produced the first recognized and documented cases of decompression sickness in man.

In an attempt to explain the affliction associated with pressure reduction, researchers turned to the laboratory and the use of a wide variety of experimental animals. In 1878, Paul Bert's book *La Pression Barometrique* summarized the information available at that time on pressure physiology. This now famous work described several decompression studies that used a variety of animal species. However, no attempt was made to use the interspecies differences for projections or estimates of the decompression requirements for man.

Not until 1908 was there a real attempt to extrapolate animal results to the formulation of decompression procedures for humans. Boycott, Damant, and Haldane (1908) suggested that ". . . the susceptibility of any animal to caisson disease after sufficiently long exposure to compressed air must depend in the main upon the rate at which its respiration and circulation removes the excess of dissolved nitrogen on decompression." They hypothesized that not only is the excess nitrogen removed faster with more rapid circulation, but that the time during which the venous blood remains in a supersaturated state is reduced. The time ". . . is so short in small animals that no bubbles at all are formed, in spite of the temporary existence of very great supersaturation in the blood and tissues. The susceptibility of any species of animals then varies enormously with the size." Further, Boycott et al. (1908) suggested that for warm-blooded animals the rate of circulation varies with ". . . the rate of respiratory exchange per unit of body weight and is therefore proportional to the ratio between body surface and body weight." They concluded by saying that the ". . . results obtained with small animals as to the time required for complete saturation, or for safe decompression, are not directly applicable to man."

This last statement was not, as many people have interpreted it, a rejection of the usefulness of animal decompression studies. On the contrary, it was a recognition that species differences exist and that mathematical expressions are needed to bridge the gap between species. Boycott et al. (1908) used goats in their decompression research; they estimated that the respiratory exchange per kilogram body weight would make the goats' saturation time about two-thirds that of man. This simple relationship has proven to be very helpful and is still used in extrapolating research on goats today. To use animal decompression studies effectively, we need similar types of functions for all of the species presently in use (Table 1). Without these bridges between species, it is difficult to assess the impact of experimental results and it is impossible to utilize laboratory research fully.

In the mid 1940's a series of animal experiments was conducted by Gersh and Catchpole. Although not intended as a study of species differences, this research contributed significantly to our understanding of these differences. A major portion of the intra- and interspecies variability can be accounted for by body fat content and gas solubility coefficients (Catchpole and Gersh 1946; Catchpole and Gersh 1947).

The most recent evaluation of species decompression differences was that of Flynn and Lambertsen (1971). These researchers demonstrated a strong log-log relationship between body weight and the dose of nitrogen that will produce an ED_{50} (the effective dose to produce decompression symptoms in 50% of the animals). They also showed that there is a shift in the relative susceptibility to decompression sickness across species. Flynn and Lambertsen state that these relationships cannot be used to project the small-animal results to man because small errors in the estimates lead to unacceptable errors in the estimation of human decompression tolerance. Their conclusions are probably correct if one is projecting data from mice to men, but if one is interested only in extrapolating to a slightly larger species, these derived relationships can be very helpful. The ability to estimate such things as the time required to reach pressure equilibrium and the pressure-reduction values needed to produce an ED_{50} is valuable because it eliminates the need to replicate entire experiments when shifting from one species to another. Development of the mathematical relationships among species allows one to estimate critical decompression parameters. The greater the similarity between species, the

TABLE 1
SPECIES USED IN DECOMPRESSION RESEARCH

Common name	Scientific name	Reference
Tadpole	–	Poiseuille (1835)
Cat	*Felis catus*	Bert (1878)
*Dog	*Canis familiaris*	*Ibid.*
*Guinea Pig	*Cavia porcellus*	*Ibid.*
House Sparrow	*Passer domesticus*	*Ibid.*
Rabbit	*Oryctolagus cuniculus*	*Ibid.*
*Rat	*Rattus norvegicus*	*Ibid.*
Snake	–	*Ibid.*
Bat	*Pipistrellus pipistrellis*	Hill and Macleod (1903)
Monkey	*Macaca mulatta*	*Ibid.*
Man	*Homo sapiens*	Boycott, Damant, and Haldane (1908)
*Goat	*Capra hircus*	*Ibid.*
*Mouse	*Mus musculus*	*Ibid.*
Duck	*Anas* sp.	Margaria, Talenti, and Sillani (1942)
Frog	*Rana pipiens*	Harris, Berg, Whitaker, Twitty, and Blinks (1945)
Bullfrog	*Rana catesbiana*	Whitaker, Blinks, Berg, Twitty, and Harris (1945)
Fish	*Oryzias* sp.	*Ibid.*
Frog	*Hyla* sp.	*Ibid.*
Hen	*Gallus gallus*	*Ibid.*
Salmon	*Oncorhynchus kisutch*	Casillas, Miller, Smith, and D'Aoust (1975)
*Kangaroo Rat	*Dipodomys* sp.	Hills and Butler (1978)
Potoroo	*Potorous tridactylus*	Hempleman (personal communication, 1977)

*Species in current use.

more precise the estimates can be. For quantum jumps between species the estimates may be less precise, but at least they provide best-estimate approximations.

The purpose of this research was to derive a set of mathematical relationships for estimating and extrapolating basic decompression parameters. These parameters included 1) time to saturation, 2) pressure-reduction limits, 3) changes in pressure-reduction limits associated with increased pressure, 4) gas-elimination time, 5) optimum decompression stop-times, and 6) time to onset of decompression symptoms. This paper is not intended to promote any particular theory or model of decompression; its sole purpose is the compilation of existing experimental decompression data. The extrapolations between species are not based upon any preconceived theoretical biases; they are simply empirically derived relationships. Individual readers may interpret the results within their own theoretical framework, be it constant volume, thermodynamic, or neo-Haldanian.

METHOD

Data sources

The numerical values used in deriving the interspecies decompression relationships were obtained from studies done in our laboratory and from data reported in the open literature. Seven different species were included in this evaluation. Their selection was based upon the amount of decompression information available on each species. The physiological data for each species used in the calculation of the extrapolation formula and the sources of the information are shown in Table 2. There is a wide variability associated with each of the numerical values in Table 2. Aware of this variation but recognizing the need for single values for a single solution of the required equations, the authors selected what they believed were the best estimates for each individual species.

The physiological parameters included in Table 2 were selected because they were readily available in the biological data books to any investigator. The respiratory exchange (RE) per unit of body weight is included because of Haldane's original suggestion that this was the differentiating factor among species. The formula used for calculating this quotient is:

$$RE = \frac{\text{tidal volume (ml)} \times \text{respiratory rate (breaths/min)}}{\text{body weight (kg)}} \qquad (1)$$

Data on seven species (man, goat, dog, guinea pig, rat, hamster, and mouse) were available for two decompression parameters: time for the body to equilibrate (saturation time) after an

TABLE 2
SPECIES FOR WHICH DECOMPRESSION INFORMATION IS AVAILABLE

	Decompression Variables				Physiological Variables		
Species	ED_{50} Saturation Pressure, ATA	Time to Saturate, min	Weight, g	Heart Rate, beats/min	Respiration Rate, breaths/min	Total Body Water, ml/kg	Respiratory Exchange/Body Weight, $\frac{\text{(ml)} \times \text{(breaths/min)}}{\text{kg}}$
Man	2.2	720	78000	72	12	635	.110
Goat	2.7	300	33000	90	19	690	.173
Dog	3.3	250	12000	115	22	628	.270
Guinea Pig	6.0	163	520	280	90	727	.339
Rat	6.8	130	250	325	97	666	.429
Hamster	7.6	90	91	450	74	674	.667
Mouse	13.8	40	22	534	163	727	1.190

Information on the decompression variables taken from: Van der Aue, Kellar, Brinton, Barron, Gilliam, and Jones (1951); Eaton and Hempleman (1962); Reeves and Beckman (1966); Reeves and Workman (1969); Buckles and Hardenbergh (1970); Flynn and Lambertsen (1971); Berghage et al. (1975); Berghage et al. (1976); Berghage, Donelson, and Gomez (1978); Berghage, Goehring, and Donelson (1978). Physiological values are best estimates based upon data taken from: Altman and Dittmer (1966, 1974); Swenson (1970); Guyton (1976).

increase in hydrostatic pressure, and the maximum exposure pressure from which an abrupt return to 1 ATA can be tolerated ("surfacing tissue values"). Data for two additional parameters, changes in pressure-reduction limits associated with increased pressure and time to the onset of decompression symptoms, were available for man, rat, and mouse. Data on rats are currently available for two other decompression parameters, gas-elimination time and optimum decompression stop time. Data on these last two decompression parameters are included in this report to indicate an area in which additional animal decompression research is needed.

Equation derivation

Least-squares regression was used to determine the best-fit equation that maximized the correlation between variables. The resulting equations were combined by trial-and-error to allow extension of their applicability to combinations of variables, e.g., allowable pressure-reduction limits for different species exposed to different pressure levels. The estimates produced by these combined equations were evaluated by correlating them with the actual values of Table 2.

RESULTS AND DISCUSSION

The initial evaluation of the data in Table 2 involved determining the intercorrelations among the seven variables. Unlike the usual intercorrelation matrix, the correlation coefficients shown in Table 3 are not all linear relationships. They are the maximum correlation coefficients that can be obtained by using a linear, an exponential, or a power function. It is obvious from the results shown in this matrix that there is high interdependence among the variables. The only low correlations in the matrix are those for total body water. The results from this initial analysis were encouraging in that they demonstrated a strong relationship between the physiological measures and the decompression parameters. The remainder of the analysis was devoted to identifying the optimum combination of variables for predicting each of the decompression parameters.

TABLE 3

Maximized Intercorrelations Among Experimental Variables

	1	2	3	4	5	6	7
1 Weight	–						
2 Heart rate	–.99(3)	–					
3 Respiration rate	–.97(3)	.97(3)	–				
4 Total body water	–.62(3)	.61(3)	.73(1)	–			
5 Respiration exchange	–.96(3)	.96(2)	.91(3)	.57(1)	–		
6 Saturation time	.98(1)	–.95(2)	–.92(3)	–.65(3)	–.99(3)	–	
7 ED_{50}	–.99(3)	.98(2)	.97(3)	.66(3)	.98(1)	–.97(3)	–

(1) linear $y = a + bx$; (2) exponential $y = ae^{bx}$; (3) power $y = ax^b$

Time to saturation

As suggested by Haldane in 1908, the RE is the best predictor for estimating the time to reach tissue-pressure equilibrium (saturation). For the seven species reviewed for this paper, the power relationship shown in Fig. 1 appears to be appropriate. The standard error of the estimate (SEE) for this relationship is 49.1 min. This is somewhat deceiving because of the positive relationship between the magnitude of the estimate and the size of the error. The average percentage error for this relationship is about 10%. This equation is only good for the range of species tested—mice to men—but it includes the weight range of most laboratory animals. Extrapolation to elephants would produce an unacceptably large error. Tissue-pressure equilibrium is defined as that time beyond which additional exposure time produces little or no increase in decompression sickness. Figure 2 shows the results obtained in our laboratory for rats breathing both helium-oxygen and nitrogen-oxygen mixtures.

The equation shown in Fig. 1 was derived for nitrogen-oxygen breathing mixtures. To correct this time for other inert gases, one should divide the nitrogen saturation time by the following correction factors:

Saturation speed	H_2	He	Ne	N_2	Ar
Relative to N_2	3.73	2.65	1.18	1.0	0.84

These correction factors are obtained by dividing the square root of the molecular weight of nitrogen (M_{N_2}) by the square root of the molecular weight of the inert gas (M_I) in question, i.e., ($\sqrt{M_N}$ / $\sqrt{M_I}$). This relationship was suggested by Keller and Bühlmann (1965). For the results displayed in Fig. 2, this relationship means that if nitrogen saturation time is between 120 and 140 min, the helium saturation time should be between 45 and 53 min. These estimates are very close to the empirical results obtained.

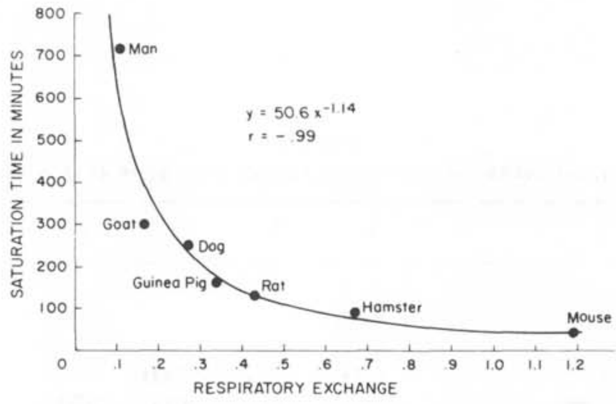

Fig. 1. Estimation of time required to re-establish tissue-pressure equilibrium after increase in pressure for various species.

$$\text{Respiratory Exchange} = \frac{\text{tidal volume (ml)} \times \text{respiratory rate (breath/min)}}{\text{body weight (kg)}}$$

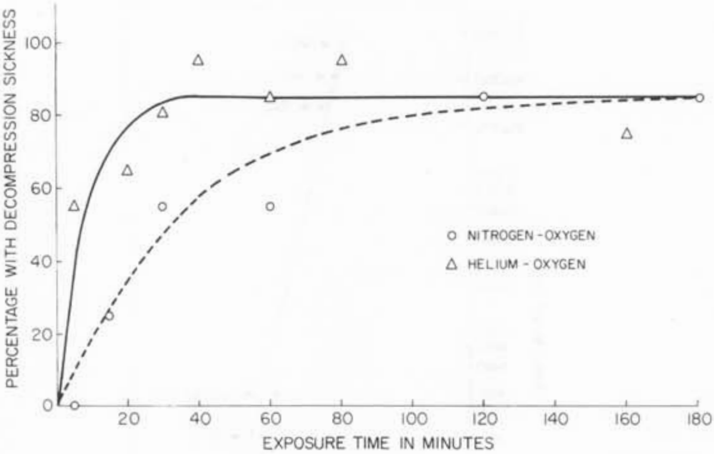

Fig. 2. Incidence of decompression sickness in rats breathing helium-oxygen and nitrogen-oxygen mixtures at 7 ATA for various lengths of time.

Pressure-reduction limits

Two physiological variables, heart rate and weight, correlate very closely with the maximum nitrogen-oxygen saturation pressure from which an organism can be abruptly decompressed to the surface. To increase the precision of this relationship, we used an ED_{50} exposure pressure rather than a bends threshold. The two physiological parameters that correlate highly with the ED_{50} pressure-reduction values are intercorrelated themselves. Either one could be used easily, but because Flynn and Lambertsen (1971) used weight, we decided to follow this precedent. The figure used by Flynn and Lambertsen was modified to include our rat data and is shown here as Fig. 3. The equation for this best fit line is

$$\triangle PED_{50} = 22.2\ W^{-.209} \qquad (2)$$

Where $\triangle PED_{50}$ = pressure reduction necessary to produce decompression sickness signs in 50% of the subjects; W = weight in grams; SEE = 0.89 atm; and $r = 0.99$.

Changes in pressure-reduction limits associated with increased pressure

There is ample evidence in the research literature that pressure-reduction limits are directly proportional to the exposure pressure. To generalize the pressure-reduction equation of the previous section, we need a correction for exposure pressure. Unfortunately, the type of information needed for such a correction is only available on three species: mice, rats, and men (Berghage, Armstrong, and Conda 1975; Berghage, Gomez, Roa, and Everson 1976; Spaur, Thalmann, Flynn, and Reedy 1976). The results of these three studies are summarized in Fig. 4. To compensate for the change in slope across species, we altered Eq. 2 as follows:

$$\triangle PED_{50} = (19\ W^{-.215}) + (1.64\ W^{-.221}) \cdot (P - 19\ W^{-.215}) \qquad (3)$$

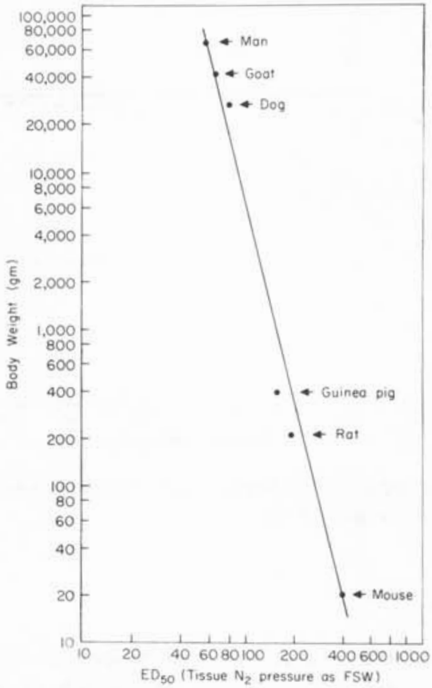

Fig. 3. Relationships between body weight and saturation pressure that will produce decompression sickness symptoms in 50% of subjects upon returning abruptly to surface.

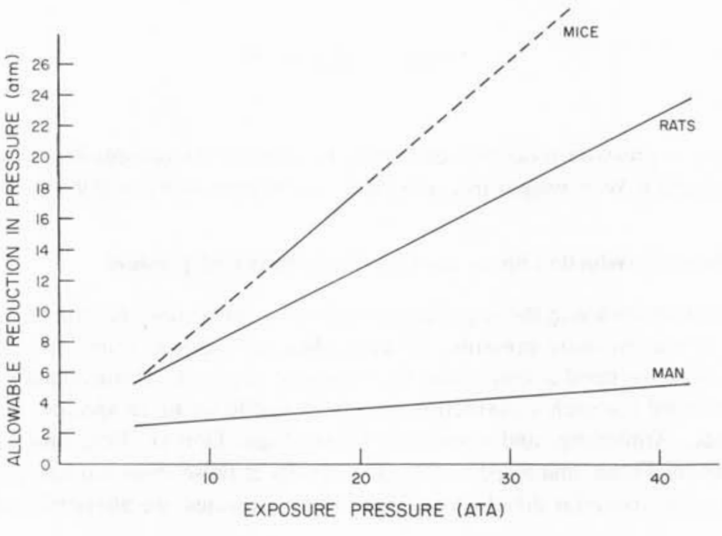

Fig. 4. Pressure-reduction values for mice, rats, and men after helium-oxygen saturation exposures at various pressures.

where $\triangle PED_{50}$ = pressure reduction necessary to produce decompression sickness signs in 50% of the subjects; W = weight in grams; P = saturation exposure pressure in ATA; SEE = 0.25 atm; and $r = 0.99$. This equation is only good for the range of species tested (mice to men) and across the saturation pressures tested (3–30 ATA).

An additional limitation of Eq. 3 is that it is only good for saturation exposures. It would be nice to be able to estimate $\triangle PED_{50}$ for any exposure time at any pressure for any species, but the data are not presently available for such predictions. Some preliminary information on the effects of time and pressure is now available for rats, but much more is needed before we can incorporate exposure time into our formula (Berghage, Goehring, and Donelson 1978).

Gas-elimination time

The studies by Hempleman (1960) and D'Aoust, Smith, and Swanson (1976) demonstrated that the decompression process interferes with gas elimination in the goat and dog. A more recent study by Berghage, Goehring, and Dyson (1978) showed that in rats gas-elimination time could be as much as 10 times longer than gas-uptake time. Because this information is only available on three different species (goat, dog, and rat), and the procedures used are not comparable, it is impossible to generalize beyond the present data. The implications of these initial data are far reaching and need to be developed further. Identical procedures need to be applied to three or more species so that the necessary extrapolation equations can be developed.

Optimum decompression stop times

Two studies in our laboratory have indicated the possible existence of optimum times for each stage of decompression. Although this initial information is only available on a single species, it has been replicated once and appears to be a reproducible phenomenon. It is important that these results be confirmed using other species so that the relationship can be developed and generalized.

Time to onset of decompression symptoms

Although not a critical variable for decompression schedule development, the time of symptom onset is important information for those working with the phenomenon. The question of concern is: how long an observation period is needed before one can be confident that one has seen all of the decompression symptoms likely to appear? Figure 5A presents the frequency distribution and cumulative-percent curve for symptom onset in the mouse. The same information is presented for rats and man in Figs. 5B and 5C. The results for all three species are summarized and generalized to other species in Fig. 6. Additional information on other species is needed to confirm this relationship.

The goal of this paper, as stated earlier, is to screen diverse animal decompression results for the purpose of producing general equations that will bridge the gaps in knowledge concerning the decompression process. Although we have been only marginally successful in our efforts, we believe that the equations presented demonstrate the existence of lawful relationships. These relationships will be helpful in extending our ability to calculate decompression risk. Through the systematic use of animal laboratory experiments, it should be possible to reduce the risk associated with the development of decompression schedules for returning human workers to normobaric pressures.

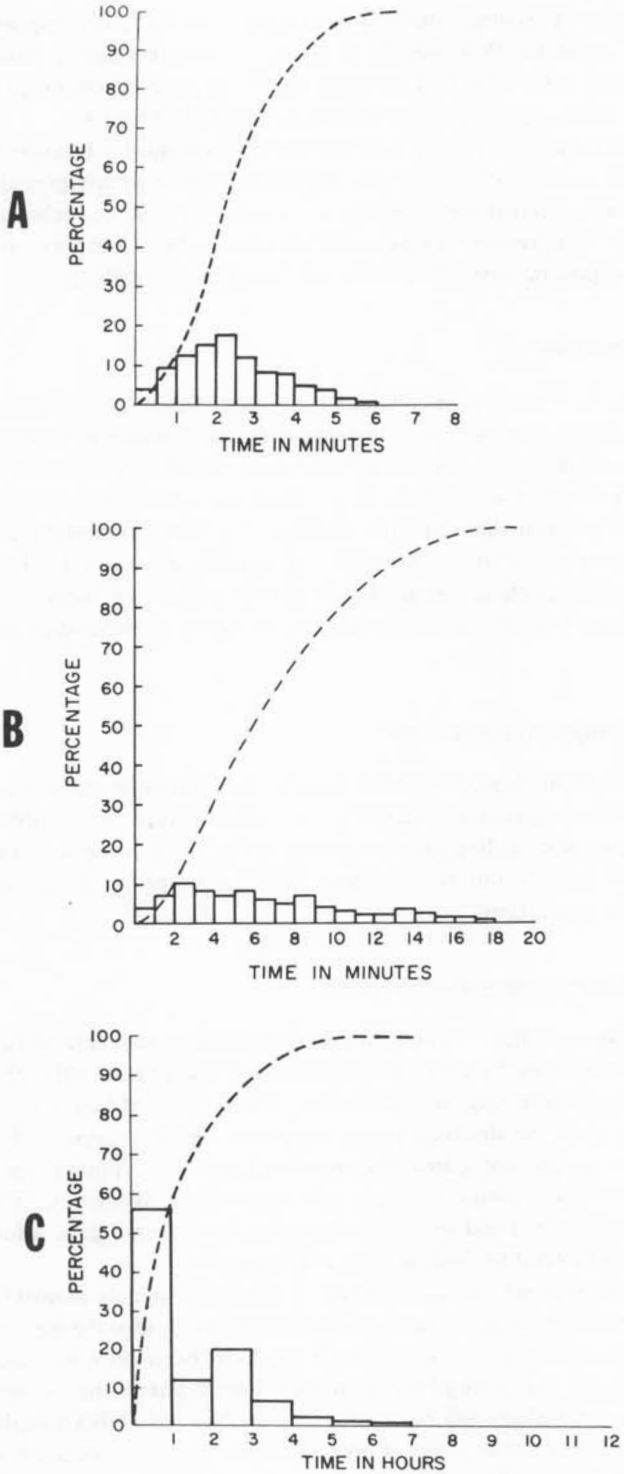

Fig. 5. Time of onset of decompression symptoms for mice (A), rats (B), and men (C).

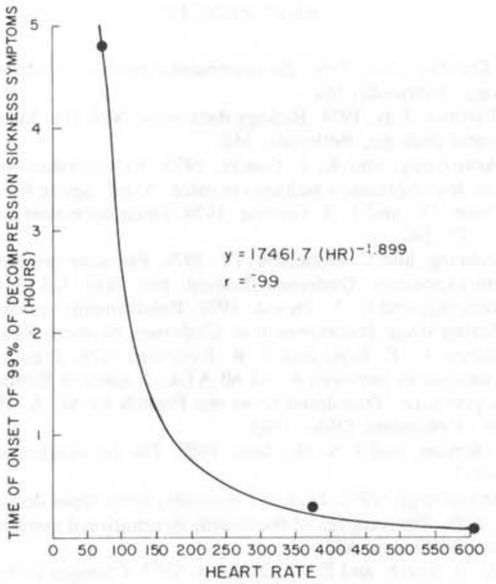

Fig. 6. Estimation of observation time necessary to detect 99% of decompression symptoms likely to occur.

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Berghage, T. E., T. D. David, and C. V. Dyson. 1979. Les différences d'espèces et la décompression. Undersea Biomed. Res. 6(1): 1–13.—Pour réconcilier les diverses travaux sur la décompression chez l'animal expérimental, on a entrepris de résumer la littérature et d'évaluer la statistique rapportée. Des animaux de vingt-deux espèces différentes ont servi de sujets expérimentaux; une statistique poursuivie n'existe cependant que pour sept espèces: l'homme, le bouc, le chien, le cobaye, le rat, le hamster, et la souris. Pour chacune des sept espèces on a crée les fonctions mathématiques basées sur les données physiologiques pour estimer: 1) le temps de saturation (le temps nécessaire au corps de s'équilibrer après exposition à une augmentation de pression hydrostatique); et 2) la limite de réduction de pression (la pression maximale d'exposition à saturation d'où l'organisme peut tolérer un retour abrupte à 1 ATA sans décompression. Les données sur l'homme, le rat, et la souris ont permis aussi de calculer les rapports de deux autres variables physiologiques de la décompression: la variation de limites de réduction de pression associées à une pression d'exposition augmentée; et la latence de l'apparition des symptômes de décompression. Enfin, on considère aussi la statistique de deux autres variables de décompression chez le rat: le temps nécessaire pour l'élimination de gaz, et le temps optimale de chaque étape de la décompression. Ces derniers variables sont discutés surtout pour encourager les travaux experimentaux sur d'autres mammifères. Les rapports physiologiques generaux que nous avons calculés servent de premier pas pour l'extrapolation parmi les espèces diverses des résultats de l'expérimentation animale sur la décompression.

animal
décompression
théorie de décompression

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