

Blood viscosity and optimal hematocrit in a deep-diving mammal, the northern elephant seal (*Mirounga angustirostris*)

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Received January 30, 1986

HEDRICK, M. S., D. A. DUFFIELD, and L. H. CORNELL. 1986. Blood viscosity and optimal hematocrit in a deep-diving mammal, the northern elephant seal (*Mirounga angustirostris*). *Can. J. Zool.* **64**: 2081–2085.

Elephant seals offer a unique opportunity to examine rheological characteristics of blood because of the normally high hematocrits in this species. A comparison of blood viscosity of the elephant seal with that of a terrestrial mammal (rabbit; HCT = 35%) reveals a threefold increase in viscosity of elephant seal blood over that of rabbit blood due to the high hematocrit (HCT = 65%). While the increased hematocrit of elephant seal blood reflects increased oxygen storage capacity, blood oxygen transport may actually be reduced by the effects of increased blood viscosity on blood flow. Elephant seal plasma viscosity was also higher than that of rabbit plasma; this was associated with a higher concentration of plasma proteins. There were no apparent differences in the viscous properties of the red blood cells of the two species. The theoretically optimal hematocrit was determined *in vitro* for reconstituted blood from each species and compared with the observed *in vivo* hematocrit. It was found that the observed hematocrit of the elephant seal lies far to the right of the predicted hematocrit for optimal oxygen transport, while the rabbit hematocrit was identical with the predicted value. These results suggest that elephant seals have increased oxygen storage capacity at the expense of optimizing oxygen transport. The observed increase in hematocrit and viscosity may be of importance in considering the diving behavior and energetics of elephant seals.

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En raison de son fort hématoците, l'éléphant de mer est l'animal idéal pour l'étude des caractéristiques rhéologiques du sang. La viscosité du sang de l'éléphant de mer est trois fois plus importante que celle d'un autre mammifère terrestre, le lapin (HCT = 35%), en raison de la valeur élevée de son hématoците (HCT = 65%). Bien qu'une telle valeur permette une augmentation de la capacité de stockage de l'oxygène, il se peut que le transport d'O₂ soit réduit, à cause des effets de l'augmentation de la viscosité sur le débit sanguin. La viscosité plasmatique de l'éléphant de mer est supérieure à celle du lapin, ce qui est dû à une plus forte concentration de protéines plasmatiques. Il n'y a apparemment pas de différence entre les propriétés visqueuses des érythrocytes des deux espèces. L'hématoците théoriquement optimal de sang reconstitué a été déterminé *in vitro* chez les deux espèces et les valeurs obtenues ont été comparées aux valeurs observées *in vivo*. L'hématoците observé chez l'éléphant de mer a une valeur située loin à droite de la valeur prédite pour un transport optimal de l'oxygène. Chez le lapin, la valeur observée coïncide avec la valeur théorique. Ces résultats semblent indiquer que les éléphants de mer ont augmenté leur capacité de stockage d'O₂ au détriment de son transport optimal. L'augmentation de l'hématoците et de la viscosité peuvent avoir une grande importance chez l'éléphant de mer et les études sur le comportement en plongée et le budget énergétique devront en tenir compte.

Introduction

The northern elephant seal, *Mirounga angustirostris*, is a deep-diving marine mammal (Scheffer 1964; Kooyman and Andersen 1969; Le Boeuf *et al.* 1986) with a hematocrit (HCT) much higher than that of most terrestrial and marine mammals (Altman and Ditmer 1964; Simpson *et al.* 1970). Anatomical (Harrison and Tomlinson 1956), cardiovascular (Elsner 1969), and physiological (Lenfant 1969; Simpson *et al.* 1970; Lane *et al.* 1972) adaptations all point to substantially increased oxygen storage capacity in elephant seals. Greater oxygen storage capability, however, may be detrimental to oxygen transport in those species with high HCTs through the effects of increased blood viscosity (Crowell and Smith 1967; Snyder 1983).

Blood viscosity and its effects on blood flow (and therefore oxygen transport) have been well studied in man and a number of terrestrial mammals (for reviews see Merrill 1969; Chien 1972). However, very little is known concerning the rheological characteristics of the blood of diving mammals (Guard and

Murrish 1975). Blood flow is inversely related to blood viscosity. Blood viscosity is, in turn, exponentially related to hematocrit. Therefore, changes in HCT may have a significant impact upon blood flow. Since blood oxygen transport is dependent upon blood flow as well as the oxygen content of the blood, oxygen transport can be shown to increase with HCT (and hemoglobin concentration) to a maximum value above which it declines as the resistance to blood flow resulting from increasing viscosity is no longer exceeded by the gain in oxygen capacity. The maximum value of oxygen transport as a function of the HCT is known as the optimal hematocrit (H_o) (Crowell and Smith 1967). For a number of terrestrial vertebrates it has been demonstrated that the predicted H_o , determined *in vitro*, is often identical with the observed *in vivo* HCT (Stone *et al.* 1968; Snyder 1971; Weathers 1976; Snyder and Weathers 1977), suggesting that terrestrial species normally maintain a HCT that maximizes oxygen transport capability. Based upon H_o theory, however, the high HCT exhibited by elephant seals, while reflecting a high oxygen storage capacity, may potentially limit cardiovascular oxygen transport and possibly aerobic scope, because of a concomitantly high blood viscosity.

This study compares blood viscosity in the elephant seal

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TABLE 1. Hematological and rheological values for rabbit and elephant seal blood and plasma (values are means \pm SE)

	<i>N</i>	HCT (%)	[Hb] (g%)	MCHC (%)	η_{bl}^* (cP [†])	η_{pl}^\ddagger (cP)	Total protein (g/dL)
<i>Oryctolagus cuniculus</i>	4	35.0 \pm 0.7	12.9 \pm 0.6	36.8 \pm 0.7	2.8 \pm 0.07	0.9 \pm 0.1	5.6 \pm 0.3
<i>Mirounga angustirostris</i>	4	65.3 \pm 2.0	24.9 \pm 0.7	38.2 \pm 0.7	8.9 \pm 0.5	1.2 \pm 0.1	6.9 \pm 0.2
Significance (<i>P</i>)		<0.001	<0.001	NS	<0.001	<0.05	<0.05

*Whole blood viscosity.

†1 P = 0.1 Pa·s.

‡Plasma viscosity.

with that in a terrestrial mammal, the rabbit (*Oryctolagus cuniculus*), and examines whether the *in vivo* HCT of the elephant seal is close to the predicted H_o determined *in vitro* as compared with a terrestrial species having a lower hematocrit.

Materials and methods

Hematology

Heparinized blood samples were drawn from four northern elephant seal yearlings housed at Sea World of California (San Diego). Three of the four blood samples were chilled and flown to Portland for analysis. The blood was analyzed within 1 day of sampling. The other blood sample was analyzed at Sea World immediately after it was drawn from the animal; there was no difference between that sample and the others analyzed in Portland. Blood from four New Zealand white rabbits was collected at Portland State University by bleeding the animals from the carotid arteries or jugular veins into heparinized tubes.

Hematocrit was determined in triplicate for whole blood samples and for reconstituted blood samples (see below) from each species by centrifugation for 5 min (Adams Autocrit). No correction was made for trapped plasma.

Hemoglobin concentration ([Hb]) of whole blood and recombined blood was determined by the cyanomethemoglobin method using bovine hemoglobin standards (Sigma).

Total plasma protein was determined on the rabbit blood by the biuret reaction using Sigma protein standard solutions (Gornall *et al.* 1949) and on the elephant seal blood by a colorimetric biuret method using Gilford system reagents (Sea World Laboratory).

Viscosity

The viscosity of whole blood was determined for a 0.2-mL sample using a Wells-Brookfield cone-plate viscometer (model LVTDCP, cone angle 0.8°). The viscometer was calibrated periodically with a 5.4-cP (1 P = 0.1 Pa·s) standard fluid (Brookfield Laboratories). The temperature of the water-jacketed sample cup was regulated at 37°C ($\pm 1.0^\circ\text{C}$) with a Forma Scientific (model 2095) constant temperature water bath. Viscosity was determined at a shear rate of 450 s^{-1} .

The blood remaining after determination of normal HCT and viscosity was centrifuged for 5–10 min to separate RBCs from plasma. Autologous plasma was then recombined in various proportions with RBCs of the same individual to obtain blood samples of different HCTs. Plasma viscosity was determined as above for each individual at 37°C.

Statistics

Values are presented as mean \pm standard error of the mean. Comparisons between mean values were determined by paired *t*-test. Exponential equations of the form $y = ae^{bx}$, were log transformed (i.e., $\ln y = \ln a + bx$) so that standard least squares linear regression techniques could be used to obtain equations for those data. Slope and elevational comparisons were determined between linear equations using analysis of covariance (Zar 1984).

Results

Hematology

The HCT and hemoglobin concentrations for elephant seal

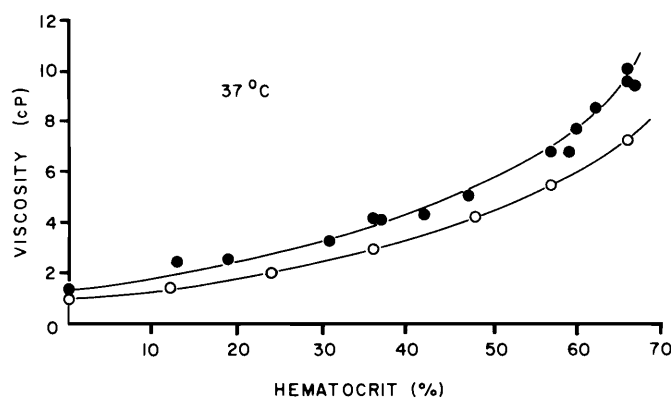


FIG. 1. The relationship between blood viscosity and hematocrit for reconstituted blood of elephant seals (closed circles) and rabbits (open circles).

blood, 65.3% and 24.9 g/dL, respectively, were significantly greater ($p < 0.001$) than the corresponding values for rabbit blood, 35% and 12.9 g/dL, respectively (Table 1). Mean cell hemoglobin concentration (MCHC), however, was not significantly different for elephant seal and rabbit blood.

Viscosity

The viscosity of whole elephant seal blood, 8.9 ± 0.5 cP, was significantly greater ($p < 0.001$) than whole rabbit blood, 2.8 ± 0.07 cP (Table 1). At physiological HCT elephant seal blood was nearly three times more viscous than rabbit blood.

The relationship between viscosity (η) and HCT is curvilinear for both elephant seal and rabbit blood (Fig. 1). The equation relating these two variables can be described as $\ln \eta = 0.26 + 0.03\text{HCT}$ ($r^2 = 0.98$; $n = 17$; $p < 0.001$) for elephant seal blood, and $\ln \eta = -0.02 + 0.03\text{HCT}$ ($r^2 = 0.97$; $n = 23$; $p < 0.001$) for rabbit blood. The slopes relating blood viscosity and HCT were identical for both species; however, the y-intercept, corresponding to plasma viscosity, was significantly greater for the elephant seal ($p < 0.05$; Fig. 1). This was also noted when plasma viscosity was directly measured independently for each species (Table 1). Elephant seal plasma also had a significantly higher concentration of total plasma proteins ($p < 0.05$; Table 1). Elevated plasma protein concentration is correlated with an increase in plasma viscosity in a number of vertebrates (Chien *et al.* 1971; Viscor *et al.* 1984).

Optimal hematocrit

Since it has been shown by several workers that oxygen transport is proportional to blood oxygen capacity divided by the resistance to flow (see Snyder 1983), oxygen transport capacity (OTC) in this study was calculated using the measured values of [Hb] and blood viscosity. Blood oxygen capacity was calculated as the product of [Hb] and the oxygen-

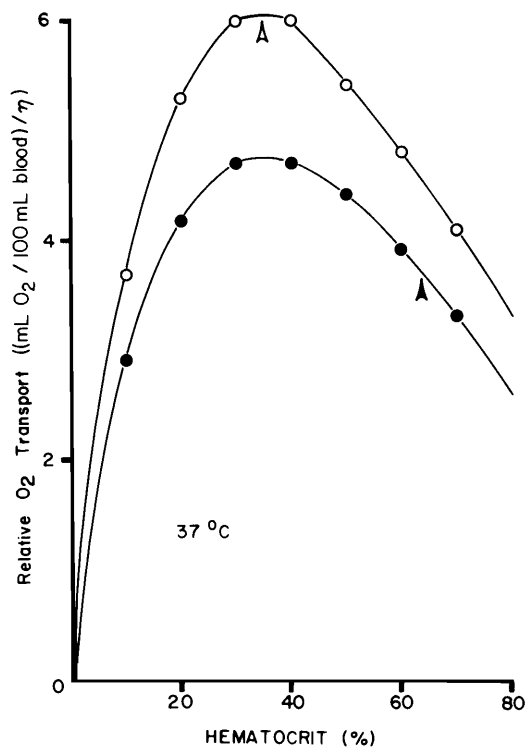


FIG. 2. Optimal hematocrit curves for elephant seal and rabbit blood. Arrowheads indicate the point on the optimal hematocrit curve that corresponds to the observed mean hematocrit for each species. Points are based on Eq. 1 in Results.

binding capacity of hemoglobin, which is typically about 1.3 mL O₂/g hemoglobin in mammals (Guyton 1981). Therefore, we used the relationship

$$[1] \quad \text{OTC} = 1.3[\text{Hb}]/\eta$$

as a means of expressing the relative oxygen transport capabilities of elephant seal and rabbit blood. Plotting OTC as a function of HCT yields characteristic H_o curves (Fig. 2).

The calculated H_o for oxygen transport is approximately 35–40% for both species (Fig. 2). At physiologic HCT, the rabbit blood matches the predicted H_o while the *in vivo* elephant seal HCT is about 70% of the predicted value for maximum oxygen transport.

Discussion

The importance of blood oxygen stores in relation to diving in elephant seals has been well established (Elsner *et al.* 1964; Bryden and Lim 1969; Simpson *et al.* 1970; Lane *et al.* 1972). A recent study of dive patterns in the northern elephant seal indicates that this species is a very deep diver, spending nearly 90% of the time underwater, with a mean dive depth of over 300 m (Le Boeuf *et al.* 1986). The maximum dive depth noted in that study was 630 m, a depth record for a pinniped species. Mean dive time was 21 min. The authors estimated that the oxygen stores available in this species would allow the animals to maintain aerobic metabolism throughout a dive of this duration. The extremely high values of HCT and [Hb] for elephant seal blood (Lenfant 1969; Lane *et al.* 1972) as compared with terrestrial mammals attest to this species' potential oxygen storage capacity. Blood volume in the northern elephant seal is greater than 20% of body weight, the highest reported for any mammal (Simpson *et al.* 1970).

A significant consequence of having a high HCT is that

blood viscosity, and hence the resistance to blood flow, also may be high. Thus blood oxygen transport to the tissues may be impaired by the viscosity effects that accompany increased hematocrit. The similarity between the slopes of the log-transformed HCT–viscosity relationship for the elephant seal and rabbit blood (see Results) indicates that, despite the threefold increase in viscosity of elephant seal whole blood over that of rabbit blood as a result of the high HCT, there is no apparent rheological mechanism by which elephant seal RBC viscosity is reduced. In fact, the increase in viscosity of elephant seal plasma over rabbit plasma (Table 1; Fig. 1) would further exacerbate the overall effect of blood viscosity on blood flow and oxygen transport rather than attenuate it.

There are two potential physiological compensations for reducing the effects of blood viscosity on blood flow: (i) increasing blood pressure, or (ii) increasing peripheral vasodilation. Van Citters *et al.* (1966) measured aortic blood pressure in resting elephant seals. Blood pressure did not appear to be different from that of other mammals at rest (e.g., 120/90: systolic/diastolic). They also demonstrated a classic diving response when the animals were forcibly submersed, i.e., bradycardia and peripheral vasoconstriction. It would seem, therefore, that elephant seals do not physiologically adjust for the effects of increased blood viscosity.

Although resting animals may be able to compensate for viscosity effects through vasomotor control, Hillman *et al.* (1985) have suggested that an increased viscosity load cannot be compensated for during maximal oxygen consumption ($\dot{V}O_{2\text{max}}$). They showed that increasing HCT beyond the normal (and optimal) HCT in *Bufo marinus* resulted in an immediate decline in systemic oxygen transport and $\dot{V}O_{2\text{max}}$. They concluded that the animals had no capacity to compensate for the increased viscosity load either by increasing blood pressure or decreasing peripheral resistance. This leads to the prediction that an animal whose HCT is not at the optimal value for oxygen transport (Fig. 2) may face an overall reduction in aerobic scope. Although there are no measurements available of $\dot{V}O_{2\text{max}}$ for elephant seals, Elsner and Ashwell-Erickson (1982) found that exercising harbor seals had an aerobic scope of about 4 times, a value somewhat lower than the 8–10 times aerobic scope predicted for mammals of similar size. Harbor seals also have relatively high HCTs (i.e., 55–60%) which may account for the unexpected reduction in aerobic scope. A similar situation may exist for elephant seals during maximal swimming efforts.

Diving behavior in marine mammal species, whether shallow or deep, slow or fast, of long or short duration, will place different constraints on their use of oxygen stores (Snyder 1983). Examination of species such as the elephant seal, which shows dramatic increases in oxygen storage capacity, suggests that there may be a trade-off between oxygen storage and oxygen transport in these very deep diving species. Where oxygen transport is compromised by increasing HCT, there may also be a concomitant reduction in aerobic scope. In other words, the diver may be able to remain submerged for long periods of time maintaining aerobic metabolism, but at the expense of rapid swimming effort. This has significance for the activity pattern of swimming both in elephant seals (Le Boeuf *et al.* 1986) and in the Weddell seal (Kooyman *et al.* 1980; Kooyman *et al.* 1981; Kooyman *et al.* 1983), also a deep-diving pinniped with substantially increased HCT and oxygen storage capacity (Lenfant *et al.* 1970; Qvist *et al.* 1981). Studies show that the Weddell seal, like the elephant seal, maximizes the time submerged relative to time spent at the surface, making dives of durations largely within the seal's

aerobic metabolism limit of 20 min (Kooyman *et al.* 1980; Kooyman *et al.* 1981; Kooyman *et al.* 1983).

Large *in situ* muscle O₂ stores in the elephant seal (Blessing and Hartschen-Niemeyer 1969) may compensate partially for poorer transport properties during diving by allowing O₂ to be sequestered, but the importance of muscle blood flow in free-diving elephant seals is not yet known. Observations from free-diving *Tursiops* suggest that muscle blood flow remains open during routine dives (Ridgway and Howard 1979). In free-diving Weddell seals, it has been observed that [Hb] actually increases over resting values and remains elevated during a dive (Qvist *et al.* 1985). If this is also true for the diving elephant seal, it may suggest an even greater potential effect of increased viscosity on oxygen transport during the dive and for the initial period of recovery.

The potential cost to maximum oxygen transport predicted by the blood oxygen capacity and blood viscosity values in the elephant seal, examined in light of the arguments for predominantly aerobic diving behavior, would suggest that given the dive times observed, this species spends its diving time swimming slowly, without the sustained or rapid bursts of speed noted in more shallow diving, surface-feeding seals (see, for example, species accounts in Ridgway and Harrison 1981). We suggest that the cost to oxygen transport projected for the elephant seal lowers aerobic scope and we predict that $\dot{V}O_{2\max}$ and swimming activity level is compromised in deep-diving marine mammal species in which adaptation to a deeper food niche includes a substantially increased hematocrit.

Acknowledgements

We thank Drs. G. K. Snyder, P. C. Withers, S. S. Hillman, and S. H. Ridgway for critically reviewing the manuscript. We also thank Dr. Jon Abramson for providing the rabbit blood. This work was supported in part by a grant from the American Philosophical Society.

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