Blood Volume and Diving Ability of the New Zealand Sea Lion, *Phocarctos hookeri*

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ABSTRACT

We test the hypothesis that the New Zealand sea lion is physiologically better equipped for prolonged, continuous diving than other otariids (fur seals and sea lions) by measuring its blood volume, an important component of its oxygen storage. Mass, hematocrit, and plasma volume were measured and blood volume calculations were completed on 14 adult females and five juvenile females. Plasma volume was determined using the Evans blue dye dilution technique. Mean plasma volume for all subjects was 74 mL kg^{-1}. Mass-specific plasma volume was significantly higher in adult females (15.3%) than in juveniles (14.6%). Blood volume (150 mL kg^{-1}) and hematocrit (51%) were not significantly different between adults and juveniles. The aerobic dive limit can be estimated by dividing the animal's oxygen stores by its metabolic rate. The estimated aerobic dive limit for adult animals was between 5.5 and 7.8 min, depending on the assumed metabolic rate. New Zealand sea lions have the highest blood volume yet reported for an otariid, which supports the hypothesis that they have a physiological capability suited to their unique diving behavior.

Introduction

The diving patterns of freely diving, air-breathing vertebrates result from an interaction between the animal's behavior and physiological capability (Castellini et al. 1985; Kooyman 1989; Ponganis et al. 1993). The animal's physiology sets an upward limit within which it must operate (Kooyman 1989; Ponganis et al. 1997). The resulting diving behavior, while being constrained by the physiological and anatomical adaptations, generally reflects the distribution, abundance, depth, and energy content of the prey (Costa 1991*a*, 1991*b*, 1993).

Recent advances in remote recorders have resulted in a wealth of information on the diving behavior of freely living marine mammals and seabirds (Kooyman 1989; Costa 1993; Boyd and Croxall 1996). These data reflect a wide range of foraging strategies among this group of vertebrates and have led to a discussion of the primary determinants of these strategies (Kooyman et al. 1980, 1983; Kooyman 1989; Costa 1993; Boyd and Croxall 1996). Evident in this discussion is a lack of basic physiological data on the parameters that govern and control the diving capability of marine mammals. The diving capability of a marine mammal is determined by its total metabolic stores and the rate at which they are used (Kooyman 1989). These metabolic stores can be separated into aerobic and anaerobic components. The aerobic component of diving metabolism is thought to be the major determinant of diving ability (Kooyman et al. 1980, 1983; Kooyman 1989; Ponganis et al. 1993, 1997). The aerobic dive limit (ADL) is experimentally defined as the diving duration beyond which blood lactate levels increase above resting levels (Kooyman 1989). ADL has only been experimentally measured in Weddell seals, *Leptonychotes weddelli*, California sea lions, *Zalophus californianus*, and white whales, *Delphinapterus leucas* (Kooyman et al. 1980, 1983; Ponganis et al. 1997; Shaffer et al. 1998). These studies found a close correspondence between measured ADL and the theoretical ADL predicted by dividing the animal's oxygen stores by its metabolic rate, which supports the importance of aerobic metabolism during diving in these species. Aerobic dives are therefore constrained by the total oxygen stored in the muscle, blood, and lung and the rate at which it is used. A significant component of the oxygen stores of marine mammals is contained in their blood. The relative importance of blood oxygen stores varies among marine mammals. For example, dolphins store 30%, otariids 54%, and phocids the most, 65%, of their total oxygen in their blood (Kooyman 1989). Given the wealth of data on diving behavior of pinnipeds and the importance of blood volume to diving ability, it is surprising that there are so few measurements on pinniped blood volume (Packer et al. 1969; Lenfant et al. 1970; Ronald 1970; Simpson et al. 1970; Aubin et al. 1978; Petrov et al. 1987; Ponganis et al. 1993, 1997; Thorson 1993; P. H. Thorson, unpublished data). Furthermore, many of these measurements were completed on a few individuals, on young animals, or on animals in captivity

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and thus may not be representative of the physiological fitness of animals in nature.

Lactating New Zealand sea lions have recently been reported to be the deepest- and longest-diving otariid (Gales and Mattlin 1997). They typically dive for 3.9 min (median = 4.3) and routinely attain depths of 123 m, with a maximum depth of 474 m. Some females routinely dive to depths of 187 m, with mean dive durations of 4.7 min. This diving pattern is characterized by almost continual dives, most of which are to the benthos. Unexpectedly, nearly half of the dives (44%) exceed the theoretical ADL. This is an unusually high proportion of dives that exceed the ADL. Aerobic diving is the most efficient way to dive, because it provides the greatest cumulative bottom time and the shortest interdive interval (Kooyman 1989; Ydenberg and Clark 1989). Gales and Mattlin (1997) hypothesized that the New Zealand sea lion is physiologically better equipped for prolonged, continuous diving than other otariids, and/or that the availability of prey is such that the diving behavior reflects the sea lions' physiological limit in a marginal foraging environment. In order to address this question, this study had two aims. The first was to quantify the plasma and blood volume of this species, and the second was to use these data to recalculate their theoretical ADL.

Material and Methods

Fieldwork was conducted at Sandy Bay, Enderby Island, Auckland Islands (50°30′ S, 166°17′ E), during January and February 1997. Enderby Island is the site of the second largest of the *Phocarctos hookeri* rookeries (ca. 400 pups yr^{-1}) (Gales and Fletcher 1998) and is the best site for capture. Individual adult and juvenile females were selected as experimental subjects on the basis of their healthy appearance. All adult females were suckling young. Captures were made using a specially designed hoop net (Furhman Diversified, Flamingo, Tex.) made from soft, strong, knotless mesh, with a multilayered head end to reduce the vision of the animal (but still allow free breathing) and a hole at the apex of the net through which the sea lion's nose protruded. Once in the net, the net handle was removed, and the sea lion was physically restrained by two handlers, who placed a rubber mask over its nose. The gas anesthetic Isoflurane was delivered with oxygen to the mask via a field portable vaporizer (Acoma MK III, Tokyo), and the sea lion was usually anesthetized within 2 min (as recommended by Gales and Mattlin [1998]). The sea lion was then strapped to a restraint frame and weighed (±0.2 kg) using a 250-kg capacity digital scale (Dyna-Link MSI-7200, Measurement Systems International, Seattle) suspended from an aluminum tripod.

Blood samples were drawn into a syringe and then decanted into a vacutainer containing lithium heparin. The initial blood sample was taken as soon as possible after physical restraint, usually before induction of anesthesia. After the initial blood samples had been taken, about 0.6 mg kg^{-1} of Evans blue dye was injected to determine blood volume (Swan and Nelson 1971; El-Sayed et al. 1995). Evans blue dye was injected into the lateral gluteal vein in a 1–3-mL volume. Upon completion of the injection and before removal of the needle, blood was withdrawn into the syringe and used to flush the contents of the syringe into the vein. This insured that the injection was intravenous and that all of the dye contained in the syringe was injected into the animal. Each syringe was calibrated gravimetrically to accurately determine the volume it contained. Blood samples were taken at 10-min intervals for up to 30 min. Once the final blood sample had been taken, the flow of anesthetic was stopped and the animal was allowed to recover. Each animal was observed after restraint.

Hematocrit (Hct) was determined in duplicate from whole-blood samples microcentrifuged for 5 min in capillary tubes at 11,500 rpm. To determine Evans blue dilution, whole-blood samples were centrifuged at 3,000 rpm for 15 min to separate plasma from red blood cells. The plasma was then microcentrifuged at 11,500 rpm to remove any remaining red blood cells and lipids from lipemic samples. A spectrophotometer was used to determine absorbance of plasma samples at 610 nm, using a preinjection plasma sample as a blank. Spectrophotometer readings were compared to dilution curves of Evans blue made with plasma. The concentration of Evans blue at equilibration was calculated as the y-intercept of the linear regression of the $\log_e$ dye concentrations versus time (El-Sayed et al. 1995). Plasma volume was calculated as: $Pv = m_i C_0^{-1}$, where Pv is plasma volume in liters, m_i is the amount of Evans blue dye injected (mg), and C_0 is the concentration of Evans blue dye in the sample at equilibration (mg mL^{-1}). Blood volume (Vb, mL) was calculated as: $Vb = Pv[100(1 - Hct)]^{-1}$.

Results

Blood volume measurements were made on 14 adult females and five juveniles. Mean mass, Hct, plasma volume, and blood volume for adult females and juveniles are shown in Table 1. Representative dilution curves obtained for this species are shown in Figure 1. Mean plasma volume for all subjects was 74 ± 4 mL kg^{-1}. Mass-specific plasma volume was significantly higher in adult females than in juveniles ($t = 2.38$, df = 17, $P < 0.05$). Blood volume (adults, 153 ± 7 mL kg^{-1}; juveniles, 146 ± 5 mL kg^{-1}) and Hct (adults 51% ± 2%; juveniles, 52% ± 3%) were not significantly different between adults and juveniles ($t = 1.81$, 1.29, df = 17, $P > 0.05$). Hct declined rapidly with time under anesthesia (Fig. 2). Blood volume was significantly correlated with body mass in adults ($r^2 = 0.90$, $P < 0.01$; Fig. 3) and juveniles ($r^2 = 0.89$, $P < 0.01$).

Discussion

The most interesting finding of this study is that the blood volume of the New Zealand sea lion is the highest yet reported

Table 1: Mass, blood volume, available O_2 stores, and estimated ADL for all subjects

	Adult Females (n = 14)	Juveniles (n = 5)
Mass (kg)	111.7 (15.4)	50.7 (5.2)
Hct (%)	51 (2)	52 (3)
Plasma volume (mL kg^{-1})	75.1 (4.1)	69.8 (4.5)
Blood volume (mL kg^{-1})	152.7 (6.7)	146.6 (4.5)
Blood O_2 (mL kg^{-1})	29.6 (1.3)	28.4 (.9)
Total O_2 (mL kg^{-1})	47.4 (2.3)	44.2 (.8)
Lower ADL (min)	3.1 (.1)	2.5 (.1)
Upper ADL (min)	8.1 (.2)	6.6 (.2)

Note. Details of calculations are given in the text. Total available O_2 stores were estimated using blood volume data from the present study as in Gentry et al. (1986). Diving metabolic rate estimated as 55.0 mL O_2 $kg^{-0.75}$ min^{-1} (Costa 1993) for lower ADL and 19.4 mL O_2 $kg^{-0.75}$ min^{-1} (Hurley 1996) for upper ADL. Values are presented as means (SD).

for an otariid, and indeed it falls well within the range reported for phocids (Fig. 4). This supports the hypothesis by Gales and Mattlin (1997) that this species is physiologically more capable of making longer, deeper, and almost continuous dives than other otariids.

The effect of a larger blood volume on the diving ability of New Zealand sea lions can be examined by determining whether, given these new data, they still routinely exceed the theoretical ADL as reported in Gales and Mattlin (1997). Gales and Mattlin (1997) calculated a theoretical ADL of 4.5 min using the regression equation presented in Gentry et al. (1986) for fur seals. This regression equation used an estimated blood volume of 10.9% and a diving metabolic rate of 27.5 mL O_2 $kg^{-0.75}$ min^{-1}. Using a blood volume of 15.3%, obtained in this study, the calculation method of Gentry et al. (1986) predicts an ADL of 6.3 min for New Zealand sea lions.

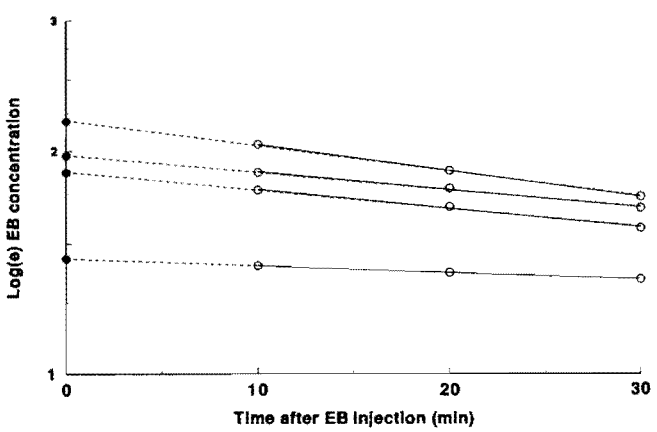

Figure 1. Examples of Evans blue (EB) dilution curves for four adult female subjects. Solid dots represent slope intercept determination of Evans blue concentration at time zero following the method of El-Sayed et al. (1995).

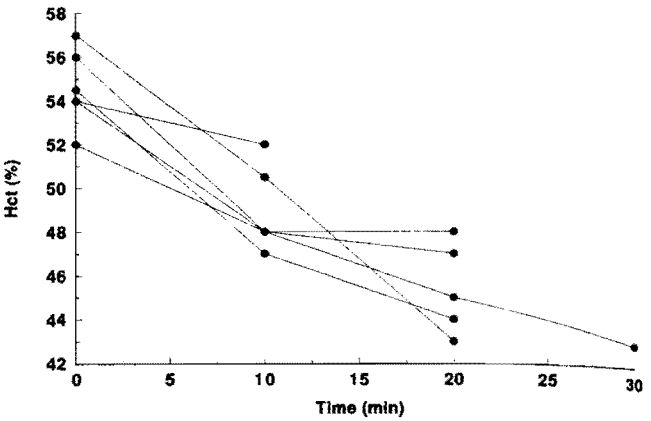

Figure 2. Changes in Hct as a function of time since anesthesia in six sea lions.

The theoretical ADL is dependent on both oxygen stores and the rate of oxygen use. Changes in diving metabolic rate profoundly influence calculations of ADL (Kooyman 1989; Castellini et al. 1992; Costa 1993; Ponganis et al. 1993). Given that there are no data on metabolic rates of New Zealand sea lions, the potential range of ADLs can be estimated using an upper and lower limit for diving metabolic rate. An upper limit of diving metabolic rate can be set from field metabolic rate data obtained from lactating sea lions and fur seals foraging at sea (55.0 mL O_2 $kg^{-0.75}$ min^{-1}) measured using doubly labeled water (Costa 1993). A lower limit of diving metabolic rate can be set from oxygen consumption measurements of California sea lions freely diving in a tank (Hurley 1996). Mean diving metabolic rate of females during 4-min dives in this study was 19.4 mL O_2 $kg^{-0.75}$ min^{-1}. These data, coupled with data on total oxygen stores, provide an ADL of between 3.1

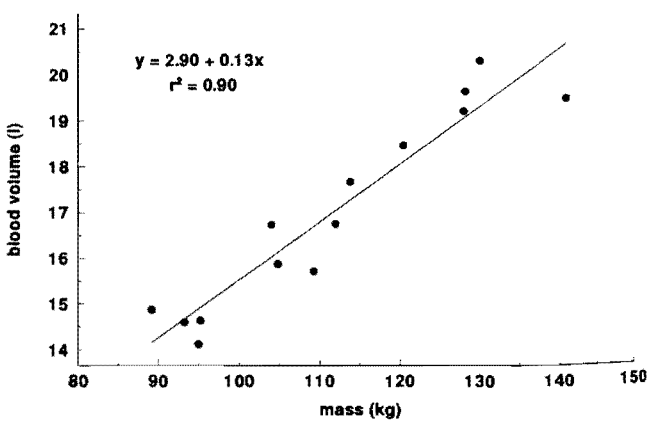

Figure 3. Relationship between blood volume and body mass for the 14 adult female New Zealand sea lions.

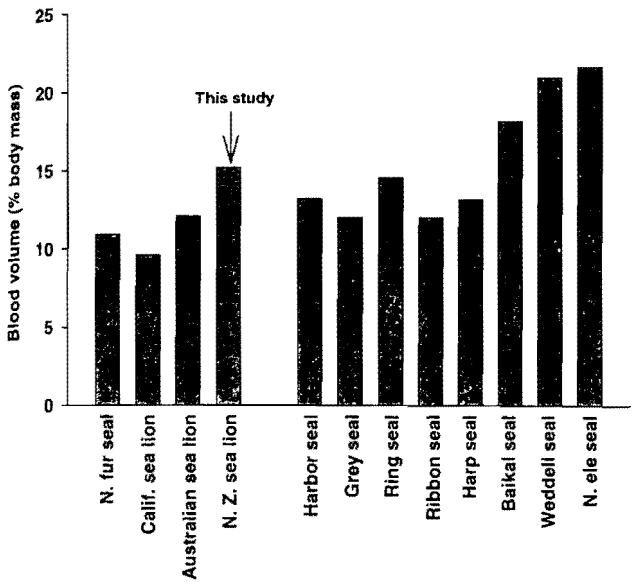

Figure 4. Summary of representative data (using comparable techniques) on blood volume as a function of body mass for pinnipeds. Data are from Lenfant et al. (1970) for northern fur seal; Ponganis et al. (1997) for juvenile California sea lion; P. H. Thorson (unpublished data) for Australian sea lion; Packer et al. (1969) for juvenile harbor seal; Castellini et al. (1985) for grey seal; Aubin et al. (1978) for ring seal and ribbon seal; Ronald (1970) for mature harp seal; Petrov et al. (1987) for Baikal seal; Ponganis et al. (1993) for Weddell seal; and Simpson et al. (1970) and Thorson (1993) for juvenile northern elephant seal.

and 8.1 min for New Zealand sea lions. For most otariids, the frequency with which they exceed their theoretical ADL is between 4% and 10% (Gentry et al. 1986; Feldkamp et al. 1989; Ponganis et al. 1990; Boyd and Croxall 1996). If this also holds for New Zealand sea lions, then an ADL at the upper limit of our range would be expected, requiring a metabolic rate at the lower end of our range. Various diving patterns will require different metabolic efforts, and thus one would expect a range of ADLs between and within species. The effect of the high blood volume reported for this species on ADL is significantly less than that of metabolic rate. Thus, this study emphasizes that increases in oxygen stores must be coupled with reductions in metabolic rate to achieve the prolonged and continuous diving observed in this species.

Variations in diving metabolic rate have important ramifications for the foraging ecology of juvenile sea lions. Although juveniles have blood volumes only 4.6% lower than adults (146 mL kg^{-1} vs. 153 mL kg^{-1}; Table 1), their smaller mass and resultant higher mass-specific metabolism cause a disproportionate reduction in ADL. The ADL of juvenile sea lions can be predicted using the relationships developed above and ranges between 2.5 and 6.6 min. Although, the blood volume of juveniles is only 4.5% lower than adults, their ADL is 19% lower. This difference results from the linear relationship between blood volume and body mass, compared to the nonlinear relationship between metabolic rate and body mass ($mass^{0.75}$; Snyder 1983). Direct measurements of ADL in juvenile Weddell seals also indicates a reduced diving capability, thought to be due to both inexperience and the scaling issues mentioned above (Kooyman et al. 1983). Given that adult females principally exploit benthic prey (Gales and Mattlin 1997) and appear to operate at or near their physiological limit, one would expect juveniles to be compromised in their ability to successfully forage at the same depth as adults. It would be interesting to know whether a lower physiological capacity for diving in juvenile sea lions results in different diving patterns, and thus the need to exploit alternative prey resources.

There are a number of potential errors associated with determination of blood volume using the Evans blue dye dilution method. First, this method only measures plasma volume and is dependent on Hct measurements for calculation of total blood volume. Hct has been shown to be highly variable and can change relative to the animal's diving state (Castellini et al. 1986, 1988; Qvist et al. 1986), as well as to the handling and immobilization techniques employed (Castellini et al. 1996). Further, Hct measurements on blood from peripheral vessels do not necessarily reflect the animal's whole-body Hct (Swan and Nelson 1971). Second, many previous studies have used a single postinjection blood sample and have failed to take into account the clearance dynamics (El-Sayed et al. 1995).

This study used free-ranging animals and employed a multiple-sampling regime. Consequently, we can have confidence in our estimation of plasma volume, but we need to be cautious interpreting comparisons with previous studies and in our calculations of total blood volume based on Hct. Even though our Hct determinations were quite consistent between individuals, an anesthetic effect was observed (Fig. 2). An equivalent reduction in Hct following Isoflurane anesthesia has been observed in Steller sea lions (Castellini et al. 1996) and Weddell seals (Ponganis et al. 1992; Hurford et al. 1996). Marine mammals have a large spleen (Ponganis et al. 1997), which, dependent on the animal's physiological state, can sequester or release red cells (Zapol et al. 1989; Ponganis et al. 1992). Anesthesia is associated with an expansion of the spleen and reduction in Hct (Ponganis et al. 1992; Hurford et al. 1996). In this study all animals were bled before any anesthetic effect but after Hct would have been maximally elevated as a result of capture-associated stress; the data are, therefore, appropriate for use in the blood volume determinations.

Given that the circulating red cell content of the blood varies with respect to the animal's physiological state, estimates of blood volume from plasma space that rely on whole-body Hct may vary relative to that measured in the peripheral circulation. In a review of blood volume measurement techniques, Swan and Nelson (1971) concluded that plasma-dilution techniques tend to slightly overestimate plasma volume and thus blood volume. In contrast, a previous study of ringed seals (Aubin

et al. 1978), where both red cell volume and plasma volume were measured, indicated that the measurement of plasma space alone underestimates total blood volume by 8%. Further, estimates of Weddell seal blood volume using measurements of both red cell and plasma volumes (Hurford et al. 1996) are very similar to those acquired by plasma volume and maximal Hct measurements alone (Ponganis et al. 1993). In this study, we followed the convention proposed by Castellini et al. (1996), who argue that maximal Hct values should be used for blood volume calculations and for interspecific comparisons of diving capability.

A further confounding variable for determining oxygen storage capacity is the positive relationship between hemoglobin content and blood volume (Snyder 1983). Given that New Zealand sea lions have increased blood volume, it would be instructive to know whether there are concomitant increases in myoglobin and hemoglobin concentrations.

In summary, determinations of blood volume in New Zealand sea lions support the hypothesis that the deep, prolonged diving pattern observed for this species is enabled by an increased oxygen storage capability. It would be interesting to know whether this species shares other enhancements that would increase its diving capability, such as higher muscle myoglobin concentration, higher blood hemoglobin concentration, a larger spleen, or a lower diving metabolic rate.

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