sucrose, and trehaloseamine). Trehalase did not utilize these substrates. Furthermore, 280 μ mole of glucose added per milliliter to the assay system did not inhibit the enzyme.

The maximal activity of the enzyme occurs at about 45°C (Fig. 3). If the enzyme is kept at 55°C for 15 minutes, then assayed at 35°C, it loses only 36 percent of its original activity, but when it is kept for 15 minutes at 60°C it loses 75 percent of its original activity. Slime-mold trehalase is more resistant to heat than purified insect trehalase (7). Purified trehalase from Neurospora is, on the other hand, even more resistant to heat; it loses negligible activity if kept at 60°C for 15 minutes (7). The purified slime-mold enzyme was stable for 6 months when kept at −20°C.

A Lineweaver-Burk plot of concentration against activity gives a value of $1.2 \times 10^{-3}M$ for the Michaelis constant (K_m) of the enzyme-substrate complex and a maximum activity of 27.2 units/mg of protein.

In general the properties of purified slime-mold trehalase resemble those of the trehalases from other sources. Its behavior on a DEAE-cellulose column is almost identical to blow-fly trehalase. Where purified trehalases have been used, trehalose is the only substrate that is utilized. The K_m of D. discoideum trehalase of $1.2 \times 10^{-3}M$ is higher than the value obtained from other purified trehalases (7).

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References and Notes

- M. Sussman and M. J. Osborn, Proc. Nat. Acad. Sci. U.S. 52, 81 (1964); B. Wright, in Biochemistry and Physiology of Protozoa, S. H. Hutner, Ed. (Academic Press, New York, 1964). p. 341
- J. T. Bonner, The Cellular Slime Molds (Princeton Univ. Press, Princeton, 1959).
- J. I. Bonner, The Cellular Slime Molds (Princeton Univ. Press, Princeton, 1959).
 V. Cochrane, Physiology of Fungi (Wiley, 1961); A. S. Sussman, Quart. Rev. Biol. 36, 109 (1961).
- G. Wyatt and G. Kalf, J. Gen. Physiol. 40, 833 (1957).
 T. Clegg and M. Filosa, Nature 192, 1077 (1977).
- T. Clegg and M. Filosa, *Nature* 192, 1077 (1961).
 C. Ceccarini and M. Filosa, *J. Cell. Comp.*
- *Physiol.*, in press. 7. E. P. Hill and A. S. Sussman, *Arch. Bioch.*
- Biophys. 102, 389 (1963); S. Friedman, *ibid.* 87, 252 (1960); G. Kalf and S. Rieder, J. Biol. Chem. 230, 691 (1958); A. Panek, *ibid.* 239, 1671 (1964).
- G. Gerish, Naturwiss. 46, 654 (1959).
 Worthington Biochemical, Glucostat procedure.
- O. H. Lowry, N. J. Rosenbrough, A. L. Farr, R. J. Randall, J. Biol. Chem. 193, 265 (1951).
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Blood Oxygen and Ecology of Porpoises of Three Genera

Abstract. Blood volumes, hemoglobin concentrations, packed-cell volumes, and heart weights were determined in three genera of propoises which differ from one another in behavior and ecology. The estimate for the total blood-oxygen content of the highly active, deep-diving, pelagic species Phocoenoides dalli was almost three times greater than that for the coastaldwelling species Tursiops truncatus, and about 70 percent greater than for the less active pelagic species, Lagenorhynchus obliquidens. Heart weights of Phocoenoides dalli were about 140 percent greater than in Tursiops truncatus and 55 percent greater than in Logenorhynchus obliquidens.

Members of the order Cetacea appear to be the best divers among the mammals. The bottlenose whale $(Hyperoodon \ rostratus)$ can remain below the surface for as long as 2 hours (1), and the sperm whale $(Physeter \ catodon)$ is evidently able to dive to a depth of at least 1000 meters (2). Some cetaceans are among the fastest swimming creatures in the sea (3). Deep dives, dives of long duration, fast swimming, and thermoregulation in cold waters may place unusual physiological requirements for oxygen transport upon these mammals.

We studied the blood volumes, heart weights, hemoglobin concentrapacked-cell tions. and volumes (hematocrit) of three genera of small cetaceans: Tursiops truncatus (Montagu), Lagenorhynchus obliquidens (Gill), and Phocoenoides dalli (True). The data were gathered over 2 years from five P. dalli (80 to 124 kg in body weight), nine L. obliquidens (60 to 110 kg), and 12 T. truncatus (62 to 155 kg). The Dall porpoises (P. dalli) that we studied are to our knowledge the only members of this species ever to survive in captivity for an extended period. Measurements of blood volume in living cetaceans had not previously been made.

Venipunctures were made in small veins on the ventral surface of the flukes. These veins are quite prominent in *L. obliquidens* and *P. dalli* but are palpable only in certain individuals of *T. truncatus*. The blood-volume measurements were made by the I¹³¹ technique (4) with a volemetron (5). The test dose, 2 ml (10 μ c), of serum albu-

min tagged with I^{131} was injected into a vein on the ventral surface of the flukes. After 10 minutes an 8-ml blood sample was drawn from a vein on the opposite side of the flukes. Packed-cell volumes (6) and hemoglobin concentrations (7) were measured each time blood volumes were measured, as well as during numerous physical examinations.

Hemoglobin concentration in P. dalli ranged from 17.8 to 23.7 g/100 ml of whole blood. In L. obliquihemoglobin concentradens the tion ranged from 16.0 to 19.6 g with a mean of 17.0 g, and in T. truncatus from 13.2 to 15.3 g with a mean of 14.4 g (Table 1). Concurrently measured packed-cell volumes ranged from 52 to 63 percent in P. dalli with a mean of 57 percent. In L. obliquidens the packed-cell volume ranged from 50 to 59 percent and the mean was 53 percent. Tursiops truncatus had a mean packed-cell volume of 45 percent with a range of 40 to 48 percent (Table 1).

Striking differences are found in blood volumes of the three species (Fig. 1 and Table 1): 143 ml/kg of body weight for *P. dalli*, 108 ml/kg for *L. obliquidens*, and 71 ml/kg for *T. truncatus*. Estimated differences in total blood-oxygen content are perhaps better indicators of the physio-



Fig. 1. Blood volume. These data were collected from two *P. dalli* females and one male, two *L. obliquidens* males and two females, and one *T. truncatus* male and three females.

Table 1. Blood volume, packed-cell volume, hemoglobin concentration, and heart weight. Heart weights were taken from our postmortem records covering stranded animals, animals which died during capture, and four that died in captivity. M, number of measurements; A, number of animals.

Blood volume (ml/kg body weight)				Packed-cell volume (%)					Hemoglobin (g/100 ml blood)				Heart weight (% of body weight)			
Mean	Range	М	A	Mean	Range	М	A	Mean	Range	М	Α	Mean	Range	М	A	
							Phoe	oenoides d	alli							
143	130-153	6	3	57	52-63	18	3	20.3	17.8–23 .7	18	3	1.31	1.25-1.34	4	4	
						I	agenorl	nyncus obli	quidens							
108	95-118	13	4	53	50-59	29	4	17.0	16.0–19 .6	29	4	0.85	0.70-0.92	5	5	
							Turs	iops trunca	tus							
71	65-83	8	4	45	40-48	81	12	- 14.4	13.2-15.3	81	12	0.54	0.50-0.56	4	4	

it can ride the bow wave if the speed

is increased to 32 km/hr, it always

veers off immediately to the side and

falls back to the wake of the ship after

logical capabilities of the species. At complete saturation each gram of hemoglobin can combine with 1.36 ml of oxygen (8). The estimated bloodoxygen capacity for a 100-kg porpoise of each species is therefore 3950 ml (27 percent by volume) for *P. dalli*, 2500 ml (23 percent by volume) for *L. obliquidens*, and 1390 ml (19.5 percent by volume) for *T. truncatus*. Thus *P. dalli* appears to have almost three times the blood-oxygen content of *T. truncatus*.

The differences in total blood volumes, hemoglobin concentrations, and estimated blood-oxygen carrying capacities appear to be correlated with the ecology of the three species of porpoise studied. Factors such as heart weight, observed swimming speed, water temperature, probable diving depth, food consumption in captivity, and blubber thickness are further indices of the differences in the three species.

Heart weights taken from our postmortem records of the three species showed *P. dalli* to have a mean heart weight of 1.31 percent of body weight in a group of three females and one male. Three *L. obliquidens* males and two females had a mean heart weight of 0.85 percent of body weight, and two *T. truncatus* males and two females had a mean heart weight of 0.54 percent of body weight (Table 1).

Norris (9) and Brownell (10) have stated that *P. dalli* appears to be the fastest swimmer of the small cetaceans they have observed, and their statement is confirmed by our observations. *Phocoenoides dalli* can overtake our capture boat at a speed of 32 km/hr, ride the bow wave at this speed for 5 minutes or more, and then accelerate rapidly ahead of the boat for 50 to 100 m before veering off to one side or the other. *Lagenorhynchus obliquidens* can overtake the boat at speeds no faster than 26 km/hr. Although

se a few minutes. *Tursiops truncatus* prefers speeds of 19 km/hr or less for bow-wave riding but is capable of speeds of about 28 km/hr for a short distance. Thus *P. dalli* appears able not only to attain a greater speed, but also to maintain this greater speed for a considerably longer period. *Phocoenoides dalli* ranges on the eastern side of the Pacific from Alaska to south-central California waters, and apparently does not occur where water

to south-central California waters, and apparently does not occur where water temperatures exceed $18^{\circ}C$ (9, 10). The Pacific white-striped porpoise, L. obliquidens, ranges in the eastern Pacific from Alaska to Baja California; these waters are relatively colder than those where T. truncatus is found.

The Atlantic bottlenose porpoise T. truncatus occurs in the Atlantic Ocean especially along the eastern and Gulf coasts of the United States, most often in shallow, inshore areas. Both L. obliquidens and P. dalli usually are found farther at sea, but L. obliquidens is occasionally seen in shallower waters. We have not encountered P. dalli in waters less than 90 m in depth. Lagenorhynchus obliquidens evidently does not dive as deeply for its food as does P. dalli, as evidenced by stomach contents of members of the two species from the same locality (9). Examinations of stomach contents of some P. dalli have revealed hake (Merluccius productus), a fish that rarely occurs above a depth of 120 m (9). This suggests that P. dalli may be a particularly deep-diving species.

In captivity, the average food requirements to maintain body weight for individuals of approximately 100 kg, eating Pacific mackerel (*Pneumatophorus diego*), are 14 kg/day for *P. dalli*, 8.5 kg/day for *L. obliquidens*, and 6 kg/day for *T. truncatus*. Food consumption in captivity suggests that P. dalli has the highest metabolic rate of the three species and thus supports the observations of the activities of these species in the wild. The four P. dalli that we dissected had much more massive skeletal musculature than members of the other two species. The P. dalli had a mean blubber thickness of about 1 cm, while L. obliquidens from the same area had a mean blubber thickness of about 2 cm, and our captive T. truncatus had a mean blubber thickness of almost 3 cm. This suggests that P. dalli may rely heavily on metabolism to maintain body temperature.

The behavior and feeding habits of a highly active, deep-diving porpoise such as P. dalli would seem to require that more oxygen be available for metabolism than is required by less active cetacean species. Tursiops truncatus is less pelagic than either P. dalli or L. obliquidens and thus probably does not require as great a capacity for oxygen transport. Lagenorhynchus obliquidens appears less active in captivity than P. dalli and, with respect to behavior and physiology, seems to be intermediate between P. dalli and T. truncatus. The highly active, pelagic species, P. dalli, has a greater blood volume and hemoglobin concentration (therefore more blood-oxygen content) and greater heart size. These adaptations seem to be correlated with its ecology. Increased capacity for oxygen transport would permit members of this species to exploit food sources occurring at deeper depths, and to pursue swift prey. It might also allow for escape from a predator such as the killer whale Orcinus orca which inhabits the same northern Pacific areas.

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References and Notes

- P. F. Scholander, Hvalradets Skrifter Norske Videnskaps-Akad. Oslo 22, 79 (1940).
 B. C. Heczen, Deep-Sea Res. 4, 665 (1957).
 C. L. Johannessen and J. A. Harder, Science 132, 1550 (1959).
- J. A. Williams and J. Fine, New Engl. J. Med. 264, 17 (1961). 4. J
- 5. Volemetron produced by Atonium Corp., Waltham, Mass.
- 6. Microhematocrit method.
- Cyanmethemoglobin method.F. W. Bernhart and L. Skeggs, J. Biol. Chem.
- 8. F.
- F. W. Bernhall and L. Skeggs, J. Dist. Contr. 147, 20 (1943).
 K. S. Norris and J. H. Prescott, Univ. Calif. Berkeley Publ. Zool. 63, 356 (1961).
- 10. R. L. Brownell, Jr., Norsk Hvaijangs, A.M., 4 (1964).
 11. We thank S. Horvath, H. N. Coulombe, and F. G. Wood, Jr.
- F. G. wood, Jr. Also at the Institute of Environmental Stress, University of California, Santa Barbara. Also at the Research Laboratory, St. John's
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Hyperphagia in Ruminants Induced by a Depressant

Abstract. Attempts at causing ventromedial hyperphagia in ruminants have been hitherto unsuccessful. In our experiments perfusion of the ventriculocisternal system with pentobarbital caused marked hyperphagia. This suggests that the ventromedial hypothalamic area is functioning in ruminants, probably as in monogastric animals, by inhibiting the lateral area.

Central organization of the regulation of food intake of ruminants is little understood; it is not necessarily identical or even closely similar to that of monogastric animals. While presence of a feeding center similar to the one found in monogastric animals is inferred from the demonstration (1)that in goats and sheep stimulation of the lateral area of the hypothalamus causes indiscriminate feeding and drinking behavior, existence of such a symmetrical ventromedial satiety center in ruminants has not been established. In monogastric animals, the ventromedial area is concerned not only with satiety but also with gastric contractions (2) and gastric juice secretion (3); anatomical and functional differences in the gastrointestinal tract of polygastric animals make such a role difficult to interpret. In monogastric animals, circulating glucose and fatty acids represent the major components of available energy, and the ventromedial satiety area is known to contain glucoreceptors (4). In ruminants the major sources of available energy are volatile fatty acids, but monitoring glucose utilization may not monitor volatile fatty-acid utilization.

Furthermore, in their natural habitat, the feed of mature ruminants has such low digestible caloric density and the process of microbial degradation and rumination is so slow and cumbersome (mean ruminal retention time is approximately 60 hours) that it appeared possible that no ventromedial satiety mechanism operated. Even in monogastric animals this mechanism does not operate during periods of active growth or during lactation (5). In a recent publication the inability to produce hyperphagia through hypothalamic lesions (though the ventromedial area was not located) is reported and this failure is ascribed to lack of distensibility of the gastrointestinal tract (6).

We reasoned that if the ventromedial area functions as a satiety center, its temporary inactivation should appear as a release of inhibition on the feeding mechanism. Since it has been shown that injection of procaine in the ventromedial area of the rat (7) or injection of pentobarbitone sodium in the lateral ventricles of the cat (8) causes transient hyperphagia, we examined the effect of pentobarbital sodium perfusion in cerebrospinal fluid of goats.

Two goats were prepared with left ventricular and cisterna magna guide tubes (9). They were fed a concentrated feed (less than 10 percent crude fiber) and about 300 g of alfalfa hay daily. Several of the pentobarbital perfusions followed a 2-hour control perfusion during which the goats ate until apparently satiated. Other perfusions were conducted following a 16hour ad libitum feeding after the ventricular and cisternal probes were placed in the goats, and after the animals received fresh feed again and were allowed to eat at will for 1 hour. Animals were placed in a chute

with a sling to help support them in the event sleep or ataxia was induced. Ventricular pressure was monitored. Perfusion rate varied between 0.5 and 1.0 ml per minute; 1 to 5 mg of pentobarbital sodium per milliliter of perfusion fluid [a synthetic cerebral spinal fluid (9)] was used.

Goats were not aware of the starting or stopping of the perfusion but they often appeared somewhat uneasy for about 1 minute, 4 or 5 minutes after the perfusion began. They then began to nibble at the concentrated feed and to increase their rate of intake which at times could be characterized only as voracious. In fact, the animals ate until their flanks were so distended at the end of an induced feeding that they appeared to be suffering from bloat. The rate of intake depended on rate of perfusion, concentration of pentobarbital sodium, the stage at which perfusion was stopped. and the rate of onset of drowsiness and sleep. Table 1 presents the feedintake data. The goats ate for varying lengths of time; a maximum induced feeding of over 900 g was eaten in less than an hour (they usually ate about 500 g of food in the first hour following a 48-hour fast). The quantity of pentobarbital sodium perfused. shown in Table 1, is the quantity actually injected in the animal for periods lasting from 4 to 15 minutes. During the longer intervals some of the pento-

Table	1.	Duration	of	perfusion	and	amount	of	feed	consump	ption	of	satiated	goats	with	the
ventric	culo	ocisternal s	syste	em perfuse	d wi	th pentol	oarl	bital s	odium sc	olution	n.				

		Perfu	sion	Pento-	Interval during	Feed eaten (g)	
Goat	Date	Time started	Duration (min)	perfused (mg)	feed was eaten (min)		
Hercules	8/24	1:00 p.m.	6	6	5	145	
Zeus	8/26	12:15 p.m. 1:35 p.m. 2:25 p.m.	8 6 6	13 9 9	15 20 10	582 276 98	
Hercules	9/8	8:30 a.m.	15	22	15	240	
Zeus	9/8	12:30 p.m. 2:20 p.m.	5 9	10 22	12 15	260 240	
Hercules	9/15	10:25 a.m. 11:05 a.m.	4 15	10 15	20 20	221 174	
Zeus	9/15	4:00 p.m. 4:37 p.m.	4 9	10 41	29 34	476 632	
_	9/18	12:42 p.m. 2:09 p.m.	15 15	68 68	48 27	922 460	