The heart rate - breathing rate relationship in aquatic mammals: A comparative analysis with terrestrial species

Jacopo P. MORTOLA*

Department of Physiology, McGill University, Montreal, QC, Canada H3G 1Y6

Abstract Aquatic and semi-aquatic mammals, while resting at the water surface or ashore, breathe with a low frequency (*f*) by comparison to terrestrial mammals of the same body size, the difference increasing the larger the species. Among various interpretations, it was suggested that the low-*f* breathing is a consequence of the end-inspiratory breath-holding pattern adopted by aquatic mammals to favour buoyancy at the water surface, and evolved to be part of the genetic makeup. If this interpretation was correct it could be expected that, differently from *f*, the heart rate (HR, beats/min) of aquatic and semi-aquatic mammals at rest would not need to differ from that of terrestrial mammals and that their HR-*f* ratio would be higher than in terrestrial species. Literature data for HR (beats/min) in mammals at rest were gathered for 56 terrestrial and 27 aquatic species. In aquatic mammals the allometric curve (HR=191·M^{-0.18}; M= body mass, kg) did not differ from that of terrestrial species (HR=212·M^{-0.22}) and their HR-*f* ratio (on average 32±5) was much higher than in terrestrial species (5±1) (P<0.0001). The comparison of these HR allometric curves to those for *f* previously published indicated that the HR-*f* ratio was body size-independent in terrestrial species while it increased significantly with M in aquatic species. The similarity in HR and differences in *f* between aquatic and terrestrial mammals agree with the possibility that the low *f* of aquatic and semi-aquatic mammals may have evolved for a non-respiratory function, namely the regulation of buoyancy at the water surface [*Current Zoology* 61 (4): 569–577, 2015].

Keywords Allometry, Breathing pattern, Control of breathing, Diving, Cardio-respiratory coupling

In mammals, resting breathing frequency (f) decreases with increasing species' body mass (M) approximately as M^{-0.25} (Guyton, 1947; Stahl, 1967). A similar allometric pattern has been reported for other time-related physiological variables, including heart rate (Mortola and Lanthier, 2004). Hence, at rest f and HR change with body size approximately in parallel, with HR about 4 times higher than f. With respect to f, aquatic species are known to deviate substantially from the general mammalian allometric pattern. Resting f of manatees, dolphins and a few species of seals varies between 1 and 7 breaths/min (Scholander and Irving, 1941; Andersen, 1966; Spencer et al., 1967; Gallivan, 1980; Andrews et al., 2000; Le Boeuf et al., 2000; Mann and Smuts, 1999), which is much lower than the f of terrestrial species of similar M. Indeed, the allometric curve constructed from 29 species of aquatic and semi-aquatic mammals spanning several orders of magnitude in body M was M^{-0.42}, drastically different from that of terrestrial species (M^{-0.25}; Mortola and Limoges, 2006). The difference from terrestrial species is small or absent for smaller mammals (about 10 Kg or less), while it becomes progressively more apparent in medium-size and larger mammals.

It is possible that the difference in *f* between aquatic and terrestrial species reflects aspects of adaptation of the control of breathing relevant to the diving and breathholding necessities of life in water (Tenney and Boggs, 1986; Bartlett, 1988) or as a response to the hydrostatic pressure (Andrews et al., 2000). However, it is unclear why these adaptations should apply only to aquatic mammals of medium or large size. Recently, Mortola and Limoges (2006) proposed that the slower f was related to a non-respiratory function of the lungs, a consequence of the breath-holding breathing pattern characteristic of aquatic species to maintain elevated lung volume to improve buoyancy. In fact, the buoyancy of mammals in water results from a variety of factors including their body fats and blubber, the air in the lungs and the air trapped in the hairs of the skin. This latter loses relevance with increased body size, because of the decrease in surface-mass ratio. As a consequence, keeping lung volume elevated to improve buoyancy may be important for larger mammals; at the same time, the increase in mean lung volume decreases f through the Hering-Breuer reflex (Widdicombe, 1961; Milsom,

Received May 28, 2014; accepted Sep. 22, 2014.

^{*} Corresponding author. E-mail: jacopo.mortola@mcgill.ca © 2015 Current Zoology

1990). Hence, based on this interpretation the control of buoyancy, a non-respiratory function, would be responsible for the low-*f* breathing of aquatic mammals.

Whether or not the heart rate (HR) of aquatic species differs systematically from that of terrestrial species is not known. If optimization of the coupling between respiratory and cardiovascular gas convection required a close matching between cardiac and respiratory rates, it is conceivable that HR of aquatic species may deviate from that of terrestrial species approximately in the same way as f does, maintaining the typical HR-f ratio of ~4. Alternatively, if the low-f breathing pattern evolved for a non-respiratory function such as the control of buoyancy, HR of aquatic species may be similar to that of terrestrial mammals of similar size; in which case, the resting HR-f ratios of aquatic species may reach unusually high values. The aim of the present study, therefore, was to use published data to construct the allometric curves of HR for aquatic and terrestrial mammals and compare them to the corresponding curves of f.

1 Materials and Methods

All HR values, for both terrestrial and aquatic species,

Ta	bl	le :	1	Resting	heart	rate	e in	terrest	trial	mamma	S
----	----	------	---	---------	-------	------	------	---------	-------	-------	---

were gathered from the literature (Tables 1 and 2). Most data included in the analysis were collected on conscious animals in resting conditions; those data collected on animals under sedation are indicated in the Tables. Owing to the scope of the study, preference was given to HR data collected in medium-size and larger species because differences in f between terrestrial and aquatic mammals begin to be apparent at M > 5-10 kg (Mortola and Limoges, 2006). Data were excluded if they originated from animals under anaesthesia, in hibernation or torpor; in addition, Monotremes and Marsupials were excluded because of their characteristically low body temperature and metabolic rate (Dawson, 1989; Brice, 2009). In case of multiple values or ranges of values, means were calculated. When there was more than one source of data for a particular species, averages were obtained. Body mass (M), if not reported, was obtained from standard bibliographic references for that sex and age (e.g., Silva and Downing, 1995).

Values are presented as means ± 1 *SEM*. Exponents (b) and intercept (a) of the allometric equation relating HR (beats/min) to M (kg) were derived from a least-squares regression analysis of the log-transformed equation $Y = a \cdot M^b$. Critical values of the correlation

Common and scientific names	M (kg) HR (bp)		references and notes
Artiodactyla			
Alpine ibex Capra ibex	92	70	Signer et al., 2011.
Asian buffalo Bubalus bubalis *	810	36.4	Lacuata and Libo, 1983.
Bighorn sheep Ovis canadensis *	98	63	Johnston et al., 1980; MacArthur et al., 1979, 1982; Harlow et al., 1987; Weisenberger et al., 1996.
Camel (Camelus) ^a *	545	49	Rezakhani and Szabuniewicz, 1977.
Cattle Bos taurus *	520	59	Ishikawa et al., 1990; Merck, 2012.
Dik-dik antelope Rhynchotragus kirkii *	4.8	114	Kamau and Maloiy, 1982.
Domestic goat Capra aegagrus hircus *	24.5	75	Merck, 2012.
Gaur Bos gaurus	520	53.5	Thomas et al., 1996.
Gemsbuck Oryx gazella	120	47	Wassenaar, 1993 [sedated].
Giraffe Giraffa camelopardalis *	525	160	Wassenaar, 1993 [sedated].
Mountain gazelle Gazella gazella	21.5	105	Furley, 1986 [immobilized].
Mule deer Odocoileus hemionus *	72	57.7	Weisenberger et al., 1996.
Muskox Ovibos moschatus *	265	57.5	Glover and Haigh, 1984.
Pig Sus domesticus *	308	95	Merck, 2012.
Roe deer Capreolus capreolus	20.7	104	Santamarina et al., 2001.
Sheep Ovis aries *	53.3	96	Reefmann et al., 2009; Merck, 2012.
Wild water buffalo Bubalus arnee	810	49.5	Ishikawa et al., 1990.
Yak Bos grunniens *	465	53	Singh et al., 1989; Krishnan et al., 2009.
Carnivora			
Badger Taxidea taxus	8.5	115	Harlow, 1981.

Continued Table 1

Common and scientific names	M (kg)	HR (bpm)	references and notes
Black bear Ursus americanus *	76.6	66	Folk, 1967.
Cat domestic Felis catus	4	113	Gompf and Tilley LP, 1979; Merck, 2012.
Dog Canis familiaris *	18.1	104	Matsunaga et al., 2001; Merck, 2012.
European polecat Mustela putorius *	1	282	Tumanov and Sorina, 1999.
Fennec Vulpes zerda	1	133	Noll-Banholzer, 1979.
Lion Panthera leo *	165	115	Wassenaar, 1993 [sedated].
Meerkat Suricata suricatta	5	190	Wassenaar, 1993 [sedated].
Mink Mustela vison	1	261	Gilbert and Gofton, 1982.
Siberian tiger Panthera tigris altaica	220	82	Wassenaar, 1993 [sedated].
Sloth bear Melursus ursinus	90	56	Wassenaar, 1993 [sedated].
Steppe polecat Mustela eversmanii *	1.5	257	Tumanov and Sorina, 1999.
Syrian brown bear Ursus arctos syriacus	250	70	Wassenaar, 1993 [sedated].
Chiroptera			
Gould's long-eared bat Nyctophilus gouldi	0.009	530 ^b	Currie et al., 2014.
Lagomorpha			
European rabbit Oryctolagus cuniculus	3.05	244	Akita et al., 2002; Merck, 2012.
Perissodactyla			
Donkey Equus africanus asinus *	178	42	Yousef and Dill, 1969.
Horse, Equus caballus *	592	37.9	Evans et al., 1976; Merck, 2012.
Zebra (Equus) ^a *	109	145	Wassenaar, 1993 [sedated].
Primata			
Baboon (Papio) ^a	10	130	Morishima and Gale, 1972.
Bonnet macaque Macaca radiata *	5	170	Reite and Short, 1986.
Capuchin monkey Cebus albifrons	1	165	Winget et al., 1968.
Chimpanzee (Pan) ^a	50.2	114	Wassenaar, 1993 [sedated].
Cotton top tamarin Saguinus oedipus	0.32	220	Hampton, 1973.
Crab-eating macaque Macaca fascicularis	5	179	Toback et al., 1978.
Human Homo sapiens	72	69.3	Mortola and Lanthier, 2004 (for references).
Orangutan Pongo borneo	100	110	Wassenaar, 1993 [sedated].
Patas monkey Erythrocebus patas	6	165	Wassenaar, 1993 [sedated].
Pigtail macaque Macaca nemestrina	6	174	Reite and Short, 1980.
Rhesus macaque Macaca mulatta	3.58	137	Fuller et al., 1996 – Malinow et al., 1974.
Saddleback tamarin Saguinus fuscicollis	0.31	190	Hampton, 1973.
Talapoin monkey (Miopithecus) ^a	1.04	233	Wassenaar, 1993 [sedated].
Proboscidea			
African elephant Loxodonta africana *	3437	32.5	Geddes LA, 2002 °; Merck, 2012.
Indian elephant, Elephas maximus indicus *	5000	35.5	Yathiraj et al., 1992.
Rodentia			
Brown rat Rattus norvegicus *	0.27	319	Mortola and Lanthier, 2004 (for references); Merck, 2012.
Guinea pig Cavia porcellus *	0.62	252	Akita et al., 2001; Merck, 2012.
Hoary marmot Marmota caligata	5.5	92	Folk et al., 2008.
House mouse Mus musculus *	0.025	552	Gehrmann et al., 2000; Tankersley et al., 2002.
Syrian hamster Mesocricetus auratus *	0.12	407	Refinetti and Menaker, 1993; Merck, 2012.

When species name was not available from the original source, only the genus is indicated. M, body mass, kg. HR, heart rate, beats per min.^a the author did not specify the species name. ^b 10°C ambient temperature. ^c the author did not specify which species of the *Loxodonta* genus; from body mass and other information it was probably *Loxodonta africana*. *, species with data for both HR and breathing frequency (Fig. 2).

Common and scientific names	M (kg)	HR (bpm)	references		
Artiodactyla					
Hippopotamus Hippopotamus amphibious *	1770	95	Elsner, 1966.		
Carnivora					
Antarctic fur seal Arctocephalus gazelle *	100	71	Salwicka and Stonehouse, 2000.		
Australian fur seal Arctocephalus pusillus d. *	24	99	Deacon and Arnould, 2009 [9-month old].		
California sea lion Zalophus californianus *	28	108	Ponganis et al., 1991. Williams et al., 1991.		
European mink Mustela rutreola *	0.7	222	Tumanov and Sorina, 1999.		
Harbor seal Phoca vitulina *	26	155	Greaves et al., 2004, 2005.		
Harp seal Pagophilus groenlandicus *	48	106	Lyamin et al., 1989.		
Hooded seal Cystophora cristata *	250	45	Kvadsheim et al., 2010.		
Northern elephant seal Mirounga angustirostris *	1038	72	Bartholomew, 1954; Le Boeuf et al., 2000.		
Polar bear Ursus maritimus *	230	50	Ørtsland et al., 1977; Folk et al., 2008.		
Sea otter Enhydra lutris *	11	139	Galantsev and Maminov, 1979.		
Southern elephant seal Mirounga leonine *	1973	53	Salwicka and Stonehouse, 2000.		
Steller sea lion Eumetopias jubatus	800	86	Hindle et al., 2010.		
Weddel seal Leptonychotes weddellii *	362	48	Kooyman and Campbell, 1972; Zapol et al., 1979; Kooyman GL, 1985; Salwicka and Stonehouse, 2000; Fuse et al., 2012		
Walrus Odobenus rosmarus *	227	90	Lyamin et al., 2013.		
Cetacea					
Beluga whale Delphinapterus leucas *	597	55	Galantsev et al., 1991; Lyamin et al., 2011.		
Bottlenose dolphin Tursiops truncates *	158	97	Galantsev et al., 1983; Williams et al., 1993; Noren et al., 2012.		
California gray whale Eschrichtius robustus	5552	28	Ponganis and Kooyman, 1999.		
Humpback whale Megaptera novaeangliae	30000	33	Wassenaar, 1993.		
Killer whale Orcinus orca *	2883	60	Spencer et al., 1967.		
Monotremata					
Platypus Ornithorhyncus anatinus	1.6	145	Evans et al., 1994.		
Rodentia					
Beaver Castor Canadensis *	22	136	Gilbert and Gofton, 1982; McKean, 1982.		
Muskrat Ondatra zibethicus	1.3	225	Gilbert and Gofton, 1982.		
Nutria Myocastor coypus	8	140	McKean, 1982.		
Sirenia					
Amazonian manatee Trichecus inunguis *	120	35	Gallivan et al., 1986.		
Dugong Dugong dugon *	501	75	Lanyon et al., 2010.		
West Indian manatee Trichechus manatus *	350	34	Galantsev and Mukhametov, 1984.		

Table 2	Resting	heart ra	ate in	aquatic	mammals
---------	---------	----------	--------	---------	---------

When species name was not available from the original source, only the genus is indicated. M, body mass, kg. HR, heart rate, beats per min. *, species with data for both HR and breathing frequency (Fig. 2).

coefficients r, differences between slopes or between sets of data were considered statistically significant at P < 0.05.

2 Results

Fig. 1 (top panel) presents the M(kg)-HR(beats/min) data points for all terrestrial (open red circles, n = 56) and aquatic (filled blue circles, n = 27) species. The data for the two groups overlapped extensively. The

respective allometric equations were $HR=191 \cdot M^{-0.18}$ (aquatic, r = 0.81) and $HR=212 \cdot M^{-0.22}$ (terrestrial, r = 0.90); these relationships did not differ significantly either in slope or intercept. Similarly, the HR allometric curves constructed with only the permanently aquatic species (Sirenia and Cetacea) or with only the semiaquatic species would not be significantly different from the function of the terrestrial species. For comparison purposes the bottom panel shows the previously published allometric curves of breathing frequency (f, breaths/min) for terrestrial and aquatic mammals (Mortola and Limoges, 2006). In the case of f, the allometric function of aquatic species differed visibly and significantly from the corresponding function of terrestrial species.

From the allometry of HR and *f*, the scaling pattern of the HR-*f* ratio for terrestrial species was HR/*f* = $4 \cdot M^{0.031}$; the 0.031 exponent, being close to zero, indicated that the HR/*f* ratio of 4 was size-independent. In contrast, the function for aquatic species was HR/*f* = $5.8 \cdot M^{0.24}$; in this case, the 0.24 exponent was significantly higher than zero and indicated that HR was disproportionately higher than *f*, the greater the species' M. Individual values of HR/*f* were computed for those species where there were data for both HR and *f* (Fig. 2); the HR/*f* of aquatic species averaged 32.2 ± 5.5 (*n* = 21), significantly higher (*P* < 0.001) than in terrestrial species with HR/*f* of 5.0 ± 0.8 (*n* = 27).

3 Discussion

Most of the extensive literature on cardiovascular adaptation to aquatic life has focused on the response to diving and breath-holding. Here, the primary aim of the current study was HR in resting conditions for the purpose of comparison between aquatic and terrestrial species. The results were unequivocal in showing overlap between the two allometric curves. The inter-specific pattern of HR, therefore, was in sharp contrast to that of the rate of breathing f (Fig. 1).

Aquatic mammals comprise a heterogeneous group of species with enormous taxonomic diversity and a large range in body masses, functionally and morphologically adapted to permanent or intermittent life in water, with webbed feet, blubber or water-repellent pelts and the possibility of sealing nostrils and ears in the water. Some are excellent breath-holders and divers. The current analysis included 27 aquatic and 56 terres-



Fig. 1 Top panel, allometric relationships (with 95% Confidence Intervals) of heart rate in aquatic (filled blue circles, n = 27) and terrestrial species (open red circles, n = 56)

For comparison purposes, the corresponding previously published allometric relationships of breathing frequency are shown in the bottom panel (from Mortola and Limoges, 2006).



Fig. 2 Ratio between resting heart rate (beats/min) and breathing frequency (breaths/min) (HR/f) in aquatic and terrestrial species

Symbols are individual species (n = 27 and 21 in terrestrial and aquatic, respectively). Columns indicate group average, bars are 1 SEM. Aquatic species had significantly higher HR/*f* than terrestrial species (P < 0.001).

trial species of, respectively, 6 and 8 mammalian orders, spanning in M from 9 g to 30 tons. Restriction to only permanently aquatic species or to only semi-aquatic species would not modify the conclusion that HR is indistinguishable from that of terrestrial species. This differs from what previously observed with respect to f. In fact, the scaling exponent of f was consistently lower in aquatic than in terrestrial species for the whole group and for the various subgroups of aquatic and semiaquatic species individually considered (Mortola and Limoges, 2006).

3.1 Buoyancy and the Hering-Breuer reflex

In mammals, buoyancy is increased by the air trapped in the hairs of the coat, the body fat and blubber and the air volume in the lungs; of these, only the latter can be varied and used to regulate buoyancy, not unlike the swim bladder of fish. Fur coats, in first approximation, are proportional to the body surface area; hence, their role in promoting flotation decreases with increasing body mass. Furthermore, many large aquatic mammals (Cetacea, Sirenia, Pinnipeds) have minimal or no fur coat, to decrease the drag. The density of body fat is lower than that of water and approximately the same among species (Fidanza et al., 1953). The human body has ~14% fat and an air-free density of 1.07 g/ml (Wilmore and Behnke, 1969). In aquatic mammals, the blubber raises the proportion of body fat up to 30% (Lockyer, 1991), which lowers the air-free body density to around unity. This means that a lung air volume of just a few percentages of body mass can bring the whole body to neutral buoyancy. Hence, closure of the upper airways at end inspiration or before end-expiration, by

raising mean lung volume offers an economical means of regulating buoyancy. Aquatic mammals of medium or large size while resting at the water surface (manatees, orca, dolphins) or on land (seals, sea lions) ventilate the lungs at low rates and, between breaths, maintain lung inflation above the passive volume of the respiratory system (Scholander, 1940; Spencer et al., 1967; Olsen et al., 1968; Kooyman et al., 1973; Gallivan et al., 1986; Castellini et al., 1986; Mortola and Lanthier, 1989). Whenever lung volume is above its resting state, the sustained increased activity of the pulmonary stretch receptors delays the onset of the next inspiration via the Hering-Bruer reflex, a vagal response widely demonstrated in all mammals (Widdicombe, 1961; Milsom, 1990), including the Harbor seal (Angell-James et al., 1981). In conclusion, it seems probable that the low f of aquatic species is a side effect of a breathing pattern meant to control lung volume as a buoyancy mechanism. This breathing pattern was considered to be partly a product of the expression of genetic traits (because it persisted out of water and was manifested in the newborns prior to their first diving experience), and partly a reflex response because it was accentuated by water immersion (Mortola and Limoges, 2006).

3.2 HR-f ratio

In terrestrial mammals, the HF-f ratio is approximately 4 throughout the range of body sizes. At first sight, such constancy could indicate that the HR-f ratio has some important role in preserving the coupling of the cardio-respiratory functions for gas convection. Alternatively, the inter-specific stability of the HR-f ratio could be a consequence of the scaling patterns of pulmonary ventilation \dot{V}_E and cardiac output (\dot{Q}) and of their respective stroke (SV) and tidal volumes (V_T). In fact, \dot{V}_{E} and \dot{Q} share the same inter-species scaling of about M^{0.75} while SV and V_T are both proportional to M^1 (Peters, 1983), probably because a pump is more efficient when the volume delivered at each stroke is proportional to its size. It follows that both HR (= \dot{Q}/SV) and $f(\dot{V}_E/V_T)$ scale inter-specifically approximately as $M^{(0.75-1)} = M^{-0.25}$. Hence, the constancy of the HR-*f* ratio among terrestrial species may not have a physiological meaning in itself; rather, it could be the consequence of the similar allometric relationships of minute output and stroke volume of the cardiovascular and respiratory systems. This should mean that, as long as \dot{Q} and \dot{V}_E remain tied together for the purpose of gas convection and exchange, the HR-f ratio has room to vary. The

mammalian respiratory system, unlike the cardiovascular system, has often evolved as a compromise between gas exchange duties and non-respiratory functions, like water balance, thermoregulation and sound production. In aquatic mammals the role of the lungs for buoyancy is probably a fundamental non-respiratory function, which requires a low-f breathing pattern. Despite the low f, because tidal volume/M is about three times the average terrestrial value (Mortola and Seguin, 2009) and because between breaths mean lung volume is maintained elevated, the values of alveolar ventilation and partial pressure of CO_2 in aquatic species are close to those of the terrestrial species (Mortola and Seguin, 2009). Hence, the fact that some aquatic species, by using the lungs as a buoyancy mechanism, keep the resting HR-f ratio several times higher than terrestrial species does not in any way compromise gas exchange.

In conclusion, a compilation of published data for many mammals indicates that there is no difference in HR between terrestrial and aquatic or semi-aquatic species. This similarity is in sharp contrast to what had emerged previously from analysis of f, because aquatic mammals of medium or large size when resting at the water surface or ashore breathe more slowly than terrestrial species of comparable body size. It follows that the resting HR-f ratio of aquatic mammals can be much higher than in terrestrial species. The current results are compatible with the interpretation that the low resting fof aquatic species is the outcome of selection for a non-respiratory function of the lungs, that is, the use of lung volume to control buoyancy.

Acknowledgements I am deeply grateful to the reviewers who offered useful comments and editorial suggestions. Cosimo L. Mortola kindly provided English translations of the publications in Russian.

References

- Akita M, Ishii K, Kuwahara M, Tsubone H, 2001. The daily pattern of heart rate, body temperature, and locomotor activity in guinea pigs. Exp. Anim. 50: 409–415.
- Akita M, Ishii K, Kuwahara M, Tsubone H, 2002. The daily pattern of cardiovascular parameters in Kurosawa and Kusanagihypercholesterolemic (KHC) rabbits. Exp. Anim. 51: 353–360.
- Andersen HT, 1966. Physiological adaptations in diving vertebrates. Physiol. Rev. 46: 212–243.
- Andrews RD, Costa DP, Le Boeuf BJ, Jones DR, 2000. Breathing frequencies of northern elephant seals at sea and on land revealed by heart rate spectral analysis. Respir. Physiol. 123: 71– 85.
- Angell-James JE, Elsner R, Daly M de B, 1981. Lung inflation: effects on heart rate, respiration, and vagal afferent activity in

seals. Am. J. Physiol. 240: H190-H198.

- Bartholomew GA, 1954. Body temperature and respiration and heart rates in the Northern elephant seal. J. Mammal. 35: 211–218.
- Bartlett D Jr, 1988. Comparative aspects of upper airway structure and function. In: Mathew OP, Sant'Ambrogio G ed. Respiratory Function of the Upper Airway. Lung Biol. Health Dis. Series, ch. 2. New York, NY: Marcel Dekker, 31–45.
- Brice PH, 2009. Thermoregulation in monotremes: Riddles in a mosaic. Austr. J. Zool. 57: 255–263.
- Castellini MA, Costa DP, Huntley A, 1986. Hematocrit variation during sleep apnea in elephant seal pups. Am. J. Physiol. 251: R429–R431.
- Currie SE, Körtner G, Geiser F, 2014. Heart rate as a predictor of metabolic rate in heterothermic bats. J. Exp. Biol. 217: 1519–1524.
- Dawson TJ, 1989. Responses to cold of monotremes and marsupials. In: Wang LCH ed. Advances in Comparative and Environmental Physiology. Vol. 4, ch. 7. Berlinl: Springer-Verlag, 255–288.
- Deacon NL, Arnould JPY, 2009. Terrestrial apnoeas and the development of cardiac control in Australian fur seal Arctocephalus pusillus doriferus pups. J. Comp. Physiol. B 179: 287– 295.
- Elsner R, 1966. Diving bradycardia in the unrestrained hippopotamus. Nature 212: 408.
- Evans BK, Jones DR, Baldwin J, Gabbott GRJ, 1994. Diving ability of the platypus. Aust. J. Zool. 42: 17–27.
- Evans JW, Winget CM, De Roshia C, Holley DC, 1976. Ovulation and equine body temperature and heart rate circadian rhythms. J. Interdiscipl. Cycle Res. 7: 25–37.
- Fidanza F, Keys A, Anderson JT, 1953. Density of body fat in man and other mammals. J. Appl. Physiol. 6: 252–256.
- Folk GE, 1967. Physiological observations of subartic bears under winter den conditions. In: Fisher KC, Dawe AR, Lyman CP, Schönbaum E, South FE, Jr ed. Mammalian Hibernation, III. New York: Am. Elsevier Publ. Co., 75–85.
- Folk GE, Dickson EW, Hunt JM, Nilles EJ, Thrift DL, 2008. QT intervals compared in small and large hibernators and humans. Biol. Rhythm Res. 39: 427–438.
- Fuller CA, Hoban-Higgins TM, Klimovitsky VY, Griffin DW, Alpatov AM, 1996. Primate circadian rhythms during spaceflight: Results from Cosmos 2044 and 2229. J. Appl. Physiol. 81: 188–193.
- Furley CW, 1986. Effect of chemical immobilisation on the heart rate and haematological values in captive gazelles. Vet. Rec. 118: 178–180.
- Fuse YK, Sakamoto KQ, Sato K, Habara Y, 2012. Cardiorespiratory pattern of rest-associated apnea in a Weddell seal: A case study at an ice hole in Antarctica. Polar Biol. 35: 969–972.
- Galantsev VP, Maminov MK, 1979. Adaptive changes of cardiac automatism in the sea otter *Enhydra lutris*. Zhurnal Evolyutsionnoi Biokhimii i Fiziologii 15: 513–519.
- Galantsev VP, Mukhametov LM, 1984. On functional and structural adaptations of cardio-vascular system in the manatee *Trichecus manatus*. Zhurnal Evolyutsionnoi Biokhimii i Fiziologii 20: 288–293.
- Galantsev VP, Kupin AG, Protasov VA, Shereshkov VI, 1983. Studies of peculiarities of bioelectrical activity of the heart in

the dolphin *Tursiops truncatus*. Zhurnal Evolyutsionnoi Biokhimii i Fiziologii 19: 560–564.

- Galantsev VP, Kupin AG, Koval EZ, Kuz'min DA, Shereshkov VI et al., 1991. Studies on electrical activity of the heart in the white whale *Delphinapterus leucas*. Zhurnal Evolyutsionnoi Biokhimii i Fiziologii 27: 774–778.
- Gallivan GJ, 1980. Hypoxia and hypercapnia in the respiratory control of the Amazonian manatee *Trichecus inunguis*. Physiol. Zool. 53: 254–261.
- Gallivan GJ, Kanwisher JW, Best RC, 1986. Heart rate and gas exchange in the Amazonian manatee *Trichechus inunguis* in relation to diving. J. Comp. Physiol. B 156: 415–423.
- Geddes LA, 2002. Electrocardiograms from the turtle to the elephant that illustrate interesting physiological phenomena. Pacing & Clin. Electrophysiol. 25: 1762–1770.
- Gehrmann J, Hammer PE, Maguire CT, Wakimoto H, Triedman JK et al., 2000. Phenotypic screening for heart rate variability in the mouse. Am. J. Physiol. 279: H733–H740.
- Gilbert FF, Gofton N, 1982. Heart rate values for beaver, mink and muskrat. Comp. Biochem. Physiol. A 73: 249–251.
- Glover GJ, Haigh JC, 1984. Clinical program: Western college of veterinary medicine muskox project. In: Klein DR, White RG, Keller S ed. Proceeding of the First International Muskox Symposium. Fairbanks: University of Alaska, 4: 173–175.
- Gompf RE, Tilley LP, 1979. Comparison of lateral and sternal recumbent positions for electrocardiography of the cat. Am. J. Vet. Res. 40:1483–1486.
- Greaves DK, Hughson RL, Topor Z, Schreer JF, Burns JM et al., 2004. Changes in heart rate variability during diving in young harbor seals *Phoca vitulina*. Marine Mammal Sci. 20: 861– 871.
- Greaves DK, Schreer JF, Hammill MO, Burns JF, 2005. Diving heart rate development in postnatal Harbour seals *Phoca vitulina*. Physiol. Biochem. Zool. 78: 9–17.
- Guyton AC, 1947. Analysis of respiratory patterns in laboratory animals. Am. J. Physiol. 150: 78–83.
- Hampton JK Jr, 1973. Diurnal heart rate and body temperature in marmosets. Am. J. Phys. Anthrop. 38: 339–342.
- Harlow HJ, 1981. Torpor and other physiological adaptations of the badger *Taxidea taxus* to cold environments. Physiol. Zool. 54: 267–275.
- Harlow HJ, Thorne ET, Williams ES, Belden EL, Gern WA, 1987. Cardiac frequency: A potential predictor of blood cortisol levels during acute and chronic stress exposure in Rocky Mountain bighorn sheep *Ovis canadensis canadensis*. Can. J. Zool. 65: 2028–2034.
- Hindle AG, Young BL, Rosen DAS, Haulena M, Trites AW, 2010. Dive response differs between shallow- and deep- diving Steller sea lions *Eumetopias jubatus*. J. Exp. Mar. Biol. Ecol. 394: 141–148.
- Ishikawa N, Tajima A, Kanai Y, Homma H, Bunyavejchewin P et al., 1990. Comparative study on intrinsic heart rate and autonomic nervous tone in swamp buffaloes *Bubalus bubalis* and cattle *Bos taurus*. Jap. J. Zootech. Sci. 61: 1028–1032.
- Johnston RH, MacArthur RA, Geist V, 1980. A biotelemetry system for monitoring heart rates in unrestrained ungulates. Biotel. Pat. Monitg. 7: 188–198.
- Kamau JMZ, Maloiy GMO, 1982. The relationship between rate of oxygen consumption, heart rate and thermal conductance of

the dik-dik antelope *Rhynchotragus kirkii* at various ambient temperatures. Comp. Biochem. Physiol. A 73: 21–24.

- Kooyman GL, 1985. Physiology without restraint in diving mammals. Mar. Mammal Sci. 1: 166–178.
- Kooyman GL, Campbell WB, 1972. Heart rates in freely diving Weddell seals *Leptonychotes weddelli*. Comp. Biochem. Physiol. A 43: 31–36.
- Kooyman GL, Kerem DH, Campbell WB, Wright JJ, 1973. Pulmonary gas exchange in freely diving Weddell seals *Leptonychotes weddelli*. Respir. Physiol. 17: 283–290.
- Krishnan G, Ramesha KP, Chakravarty P, Chouhan VS, Jayakumar S, 2009. Diurnal variation in the physiological responses of jaks. Ind. J. An. Sci. 79: 1132–1133.
- Kvadsheim PH, Sevaldsen EM, Folkow LP, Blix AS, 2010. Behavioural and physiological responses of hooded seals *Cystophora cristata* to 1 to 7 kHz sonar signals. Aquatic Mammals 36: 239–247.
- Lacuata AQ, Libo RN, 1983. Electrocardiographic patterns of Philippine swamp buffalo. Phil. J. Vet. Med. 22: 76–99.
- Lanyon JM, Sneath HL, Long T, Bonde RK, 2010. Physiological response of wild dugongs *Dugong dugon* to out-of-water sampling for health assessment. Aquatic Mammals 36: 46–58.
- Le Boeuf BJ, Crocker DE, Grayson J, Gedamke J, Webb PM, et al., 2000. Respiration and heart rate at the surface between dives in northern elephant seals. J. Exp. Biol. 203: 3265–3274.
- Lockyer C, 1991. Body composition of the sperm whale *Physeter catodon* with special reference to the possible functions of fat depots. Rit Fiskideildar 12: 1–24.
- Lyamin OI, Oleksenko AI, Polyakova IG, 1989. Sleep and wakefulness in Greenland seal pups. Zhurnal Vysshei Nervnoi Deyatel'nosti Imeni I. P. Pavlova 39: 1061–1069.
- Lyamin OI, Korneva SM, Rozhnov VV, Mukhametov LM, 2011. Cardiorespiratory changes in Beluga in response to acoustic noise. Doklady Biol. Sci. 440: 275–278.
- Lyamin OI, Lapierre JL, Mukhametov LM, 2013. Sleep in aquatic species. In: Kushida C ed. The Encyclopedia of Sleep. Vol. 1. Waltham, MA: Academic Press, 57–62.
- MacArthur RA, Johnston RH, Geist V, 1979. Factors influencing heart rate in free-ranging bighorn sheep: A physiological approach to the study of wildlife harassment. Can. J. Zool. 57: 2010–2021.
- MacArthur RA, Geist V, Johnston RH, 1982. Physiological correlates of social behaviour in bighorn sheep: A field study using electrocardiogram telemetry. J. Zool. 196: 401–415.
- Malinow MR, Hill JD, Ochsner AJ, 1974. Heart rate in caged rhesus monkey *Macaca mulatta*. Lab. Anim. Sci. 24: 537–540.
- Mann J, Smuts B, 1999. Behavioral development in wild bottlenose dolphin newborns (*Tursiops* sp.). Behaviour 136: 529–566.
- Matsunaga T, Harada T, Mitsui T, Inokuma M, Hashimoto M et al., 2001. Spectral analysis of circadian rhythms in heart rate variability of dogs. Am. J. Vet. Res. 62: 37–42.
- McKean T, 1982. Cardiovascular adjustments to laboratory diving in beavers and nutria. Am. J. Physiol. 242: R434–R440.
- Merck, 2012. The Merck Veterinary Manual for Vet Professionals. http://www.merckmanuals.com/vet/appendixes/reference_guid es/resting_heart_rates.html
- Milsom WK, 1990. Mechanoreceptor modulation of endogenous respiratory rhythms in vertebrates. Am. J. Physiol. 259: R898– R910.

- Morishima MS, Gale CC, 1972. Relationship of blood pressure and heart rate to body temperature in baboons. Am. J. Physiol. 223: 387–395.
- Mortola JP, Lanthier C, 1989. Normoxic and hypoxic breathing pattern in newborn grey seals. Can. J. Zool. 67: 483–487.
- Mortola JP, Lanthier C, 2004. Scaling the amplitudes of the circadian pattern of resting oxygen consumption, body temperature and heart rate in mammals. Comp. Biochem Physiol. A 139: 83–95.
- Mortola JP, Limoges MJ, 2006. Resting breathing frequency in aquatic mammals: A comparative analysis with terrestrial species. Respir. Physiol. Neurobiol. 154: 500–514.
- Mortola JP, Seguin J, 2009. End-tidal CO₂ in some aquatic mammals of large size. Zool. 112: 77–85.
- Noll-Banholzer U, 1979. Body temperature, oxygen consumption, evaporative water loss and heart rate in the fennec. Comp. Biochem. Physiol. A 62: 585–592.
- Noren SR, Kendall T, Cuccurullo V, Williams TM, 2012. The dive response redefined: Underwater behavior influences cardiac variability in freely diving dolphins. J. Exp. Biol. 215: 2735– 2741.
- Olsen CR, Elsner R, Hale FC, 1968. "Blow" of the Pilot whale. Science 163: 953–955.
- Ørtsland NA, Stallman RK, Jonkel CJ, 1977. Polar bears: Heart activity during rest and exercise. Comp. Biochem. Physiol. A 57: 139–141.
- Peters RH, 1983. The ecological implications of body size. Cambridge: Cambridge University Press.
- Ponganis PJ, Kooyman GL, 1999. Heart rate and electrocardiogram characteristics of a young California gray whale *Eschrichtius robustus*. Marine Mammal Sci. 15: 1198–1207.
- Ponganis PJ, Kooyman GL, Zornow MH, 1991. Cardiac output in swimming California sea lions *Zalophus californianus*. Physiol. Zool. 64: 1296–1306.
- Reefmann N, Bütikofer Kaszàs F, Wechsler B, Gygax L, 2009. Physiological expression of emotional reactions in sheep. Physiol. Behav. 98: 235–241.
- Refinetti R, Menaker M, 1993. Independence of heart rate and circadian period in the golden hamster. Am. J. Physiol. 264: R235–R238.
- Reite M, Short R, 1980. A biobehavioral developmental profile (BDP) for the pigtailed monkey. Devel. Psychobiol. 13: 243– 285.
- Reite M, Short R, 1986. Behaviour and physiology in young bonnet monkey. Devel. Psychobiol. 19: 567–579.
- Rezakhani A, Szabuniewicz M, 1977. The electro cardiogram of the camel *Camelus dromedarius*. Zentralbl. Veterinaermediz. Reihe A. 24: 277–286.
- Salwicka K, Stonehouse B, 2000. Visual monitoring of heartbeat and respiration in Antarctic seals. Polish Polar Res. 21: 189– 197.
- Santamarina G, Espino L, Suarez ML, 2001. Electrocardiographic parameters of free-ranging roe deer *Capreolus capreolus*. J. Zoo Wildlife Med. 32: 441–446.
- Scholander PF, 1940. Experimental investigations on the respiration function in diving mammals and birds. Hvalradets Skr. 22: 1–131.
- Scholander PF, Irving L, 1941. Experimental investigations on the respiration and diving of the Florida manatee. J. Cell. Comp.

Physiol. 17: 169-191.

- Signer C, Ruf T, Arnold W, 2011. Hypometabolism and basking: The strategies of Alpine ibex to endure harsh over-wintering conditions. Funct. Ecol. 25: 537–547.
- Silva M, Downing JA, 1995. CRC Handbook of Mammalian Body Masses. CRC Press, Boca Raton, FL, 359 pp.
- Singh SP, Sharma KB, Rastogi SK, Narang MP, 1989. A few physiological parameters of Yak. Ind. J. An. Sci. 59: 1108–1109.
- Spencer MP, Gornall TA, Poulter TC, 1967. Respiratory and cardiac activity of killer whales. J. Appl. Physiol. 22: 974–981.
- Stahl WR, 1967. Scaling of respiratory variables in mammals. J. Appl. Physiol. 22: 453–460.
- Tankersley CG, Irizarry R, Flanders S, Rabold R, 2002. Selected contribution: Circadian Rhythm variation in activity, body temperature, and heart rate between C3H/HeJ and C57BL/6J inbred strains. J. Appl. Physiol. 92: 870–877.
- Tenney SM, Boggs DF, 1986. Comparative mammalian respiratory control. In: Cherniack NS, Widdicombe JG ed. Handbook of Physiology, Section 3: The Respiratory System, Vol. II, part 2, ch. 27. Bethesda, MD: Am. Physiol. Soc., 833–855.
- Thomas PR, Cook RA, Burney DA, Doherty JG, Koontz FW, 1996. Biotelemetric monitoring of physiological function in gaur *Bos gaurus*. J. Zoo Wildlife Med. 27: 513–521.
- Toback JM, Clark JC, Moorman WJ, 1978. The electrocardiogram of *Macaca fascicularis*. Lab. An. Sci. 28: 182–185.
- Tumanov IL, Sorina EA, 1999. Age dynamics in body weight and physiological indices in some mustelid species (Mustelidae). Zool. Rec. Small Carn. Conserv. 20: 33–37.
- Wassenaar C, 1993. Comparative Electrocardiography in Mammals: Atrioventricular Transmission and Heart Size. Thesis, University of Utrecht, Utrecht, Netherlands, pp 1–161.
- Weisenberger ME, Krausman PR, Wallace MC, De Young DW, Maughan OE, 1996. Effects of simulated jet aircraft noise on heart rate and behavior of desert ungulates. J. Wildlife Manag. 60: 52–61.
- Widdicombe JG, 1961. Respiratory reflexes in man and other mammalian species. Clin. Sci. 21, 163–170.
- Williams TM, Kooyman GL, Croll DA, 1991. The effect of submergence on heart rate and oxygen consumption of swimming seals and sea lions. J. Comp. Physiol. B 160: 637–644.
- Williams TM, Friedl WA, Haun JE, 1993. The physiology of bottlenose dolphins *Tursiops truncatus*: Heart rate, metabolic rate and plasma lactate concentration during exercise. J. Exp. Biol. 179: 31–46.
- Wilmore JH, Behnke AR, 1969. An anthropometric estimation of body density and lean body weight in young men. J. Appl. Physiol. 27: 25–31.
- Winget CM, Card DH, Hetherington NW, 1968. Circadian oscillations of deep-body temperature and heart rate in a primate *Cebus albafrons*. Aerosp. Med. 39: 350–353.
- Yathiraj S, Choudhurl PC, Rao DST, Roddy PK, 1992. Clinicohaematological observations on Indian elephant *Elephas maximus indicus*. Indian Vet. J. 69: 995–997.
- Yousef MK, Dill DB, 1969. Resting energy metabolism and cardiorespiratory activity in the burro *Equus asinus*. J. Appl. Physiol. 27: 229–232.
- Zapol WM, Liggins GC, Schneider RC, Qvist J, Snider MT et al., 1979. Regional blood flow during simulated diving in the conscious Weddell seal. J. Appl. Physiol. 47: 968–973.

Copyright of Current Zoology is the property of Current Zoology and its content may not be copied or emailed to multiple sites or posted to a listserv without the copyright holder's express written permission. However, users may print, download, or email articles for individual use.