# The Healthy Heart: Lessons from Nature's Elite Athletes

Terrie M. Williams,[1] Penni Bengtson,[2] Diana L. Steller,[3] Donald A. Croll,[1] and Randall W. Davis[4]

[1]Department of Ecology and Evolutionary Biology, University of California, Santa Cruz, California; [2]USAT Level II Certified Race Director-USAT Swim Task Force, Finish Line Productions, LLC, Boulder Creek, California; [3]Moss Landing Marine Laboratories, Moss Landing, California; and [4]Deparments of Marine Biology and Wildlife and Fisheries Science, Texas A&M University, Galveston, Texas
williams@biology.ucsc.edu

The incidence of cardiovascular disease in humans is more than three times that of many wild and domestic mammals despite nearly identical heart morphologies and responses to exercise. A survey of mammalian species from 0.002-kg shrews to 43,000-kg whales shows that the human heart is more dog-like than cat-like and that neither body size nor longevity accounts for the relative vulnerability to cardiovascular disease. Rather, a major difference is daily activity patterns, which may underlie the comparatively healthy hearts of wild mammals.

For the past decade, cardiovascular disease has maintained its distinction as the leading cause of death for humans worldwide (World Health Organization, http://www.who.int/mediacentre/factsheets/fs310/en/). The U.S. leads this trend, with more than 2,150 Americans dying of ischemic heart disease or stroke each day, a statistic that equates to one death every 40 s or 31.3% of all deaths annually (39). What is so remarkable in these statistics is that such a level of cardiovascular-related mortality is exceedingly rare among wild mammals. Overall, the incidence of heart disease generally represents <11% of deaths in adult wild mammals (31, 46). When it does occur in the wild, heart related illnesses are often associated with unique confounding conditions such as parasitic protozoan infection in the California sea otter (*Enydra lutris nereis*; Ref. 31) or low genetic diversity in the endangered Florida panther (*Felis concolor coryi*; Ref. 46). Even among our pets, surveys have shown that only 5-10% of domestic dogs and cats die of cardiovascular illnesses (4, 43), with the primary cardiac abnormality in dogs being valvular disease (http://www.merckmanuals.com/vet).

There are many plausible explanations for the prevalence of cardiovascular disease in humans vs. animals, including diet, exercise, lifestyle, longevity, and simply bad genetics (39). However, there is no a priori reason to believe that the hearts of wild mammals are biologically safeguarded compared with the human heart. From diminutive shrews to enormous elephants and whales, there is little morphological difference in the basic structure of the four-chambered mammalian heart except for overall size. This includes mammalian hearts that beat at high altitude, on every continent, and across the oceans, as well as hearts that support physiological states ranging from metabolic suspension during hibernation in marmots (*Marmota flaviventris*) to high-energy, 60 miles/h sprinting in cheetahs (*Acinonyx jubatus*). Longevity is also an unlikely underlying factor for increased mortality since the hearts of some wild mammals function for extraordinarily long periods of time. Bowhead whales (*Balaena mysticetus*), for example, have a lifespan two to three times that of humans (22), with their healthy giant hearts pumping for >200 years.

For the past three decades, our labs have examined the form and function of the four-chambered heart across the mammalian kingdom and under diverse performance demands to better understand the attributes that might contribute to cardiovascular health in wild mammals. This has included assessing general heart morphology of wild and domestic species, as well as comparing its function in extreme mammalian athletes from deep diving seals (15, 41, 57) to big wave surfers (55). The underlying questions have remained unchanged: How do the hearts of humans and wild mammals compare, and are there lessons regarding cardiac health that might be gleaned from highly active wild mammals?

## The Challenge of Lion-Hearted Athletes

The role of the heart in supporting aerobic exercise in mammals begins with its size and a concomitant ability to transport oxygen via the vascular tree. For nearly half a century, the size of the mammalian heart has generally been considered to comprise 0.6% of total body mass, regardless of species (51, 52). This proportional standard evolved from strong allometric regressions for heart mass relative to body mass across different mammalian groups. Building on the work of Brody (7), W. B. Stahl noted that the heart mass of primates, including humans as well as other mammals, could be predicted from body mass ($M_b$) according to

$$\text{Heart mass} = 0.0058M_b^{0.99} \quad (n > 100 \text{ animals}; \ r = 0.99)$$
$$(1)$$

where heart mass and $M_b$ are in kilograms (51). Stahl further suggested that this relationship may even provide a reasonable prediction for the heart mass of exceptionally large mammals such as elephants and whales. Indeed, as more species have been measured over the years, we now know that the allometric regression proposed by Stahl (51)

reasonably predicts heart mass from body mass across mammalian groups, representing eight orders of magnitude in body size from 0.002-kg Etruscan shrews (*Suncus etruscus*) to 43,000-kg sperm whales (*Physeter macrocephalus*) (FIGURE 1A; Refs. 18, 27).

On closer inspection, species-specific variance around this relationship reveals the importance of heart size in supporting overall aerobic capacity among different mammalian groups (FIGURE 1B). The proportional size of the heart in wild mammals also provides insight into preferred hunting styles. For example, canids including wolves (*Canis lupus*) and coyotes (*Canis latrans*) that chase down prey, as well as many breeds of domestic dogs bred for aerobic work, have proportionately larger hearts relative to their body mass. The mean heart mass of this carnivore group, $0.91 \pm 0.05\%$ of body mass (means $\pm$ SE; $n = 12$ across 3 wild canids and 7 domestic dog breeds), represents a 52% increase over predicted values and reflects the high aerobic scope of canids (54). Racing greyhounds, Iditarod sled dogs that perform 1,800-km treks across Alaska, and many wild canids show the highest proportional heart values within this group. They also demonstrate some of the highest relative maximum oxygen consumption rates ($\dot{V}O_{2max}$). The resulting factorial aerobic scope (calculated from $\dot{V}O_{2max}$ divided by resting metabolic rate) ranges from 10 to 25 in canids, more than double the level of less athletic species (54).

Other aerobic mammals follow similar trends in factorial scope and relative heart mass (3). Horses have a mean heart mass of $0.77 \pm 0.02\%$ of body mass ($n = 10$ breeds), and human marathoners demonstrate heart masses that are 10–33% larger than those of more sedentary subjects (8, 17). The $\dot{V}O_{2max}$ of one such elite marathoner, Clarence Del Mar, who completed more than 1,000 long-distance races in his lifetime, had an aerobic scope of 15 times resting (17), reflecting this difference in heart mass for moving oxygen.

In contrast to dogs and humans, "lion-hearted" felids may have an underlying biological explanation for appearing lethargic. The heart mass of this taxonomic group from domestic cats to tigers averages only $0.46 \pm 0.02\%$ of body mass ($n = 12$ across 1 domestic and 4 wild species), 24% lower than predicted for other mammals. Perhaps not surprisingly, we found that the $\dot{V}O_{2max}$ of mountain lions (*Puma concolor*) running on an inclined treadmill was only seven times resting metabolic rate (Williams TM, unpublished observations; Ref. 58). Similar limitations in aerobic range have been reported for immature male African lions (*Panthera leo*; Ref. 11). In terms of aerobic capacity, "lion-hearted" athletes appear to pale compared with other terrestrial mammals. Nonetheless, they
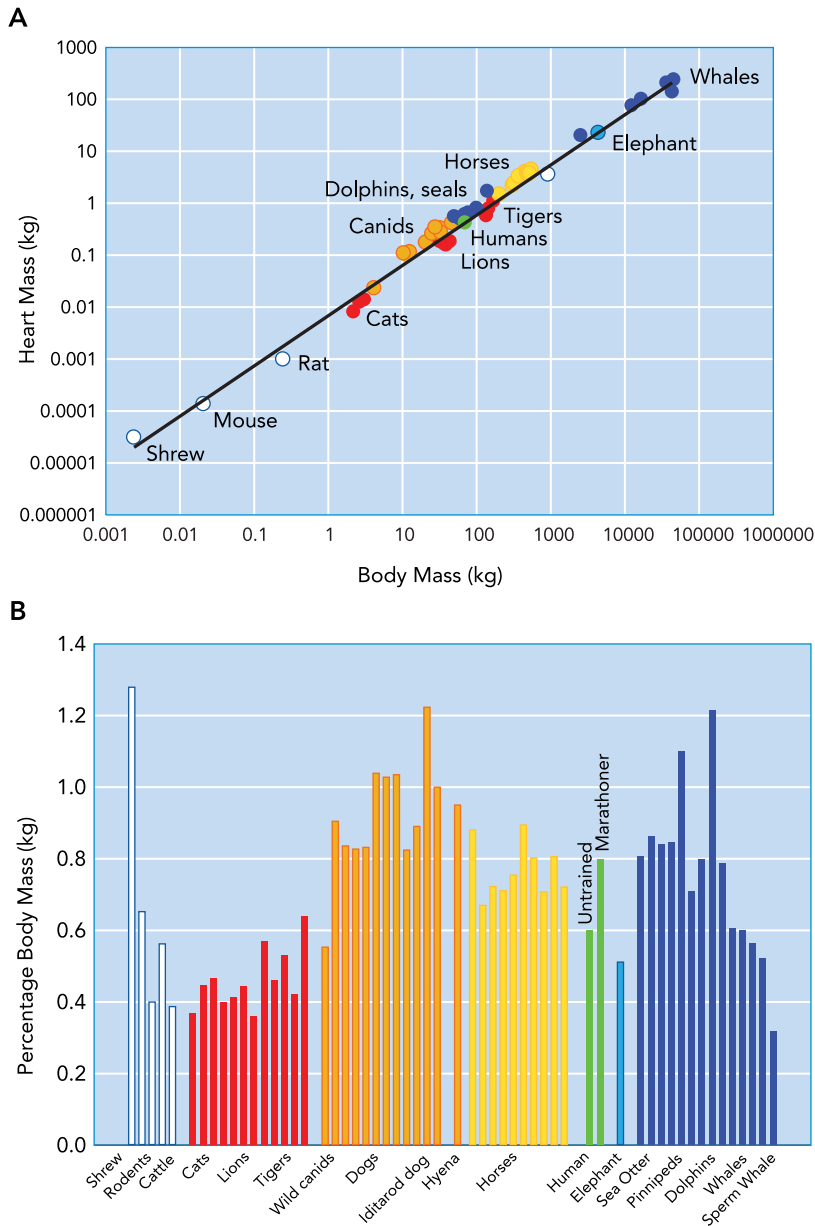


**FIGURE 1. Changes in the size of the mammalian heart across eight orders of magnitude in body mass**
*A*: the allometric relationship for heart mass in relation to body mass for rodents (white circles), felids (red), canids (orange), horses (yellow), humans (green), elephants (cyan), and marine mammals (blue). The solid line is the least squares regression from *Eq. 1* in the text. *B*: the proportional size of the heart is compared for individual species within different mammalian groups color coded as in *A*. Note the extreme proportions for the smallest (shrew) and largest (sperm whale) mammals in this study. Data sources include new measurements combined with data from McAlpine (37), Hoppeler et al. (27), Schaller (47), Gunn (24), and Mazak (36).

are still athletes. As a group, the physiology of felids is generally built for energy-conserving stalking and the anaerobic sprint and pouncing kill (58) where the selective pressure for adaptive remodeling of the heart for high aerobic capacity is comparatively low.

Although the physics of exercise differ markedly for animals moving through air and water, the size of the heart in marine mammals, as in terrestrial mammals, is dictated by allometry and aerobic demands for exercise. The magnitude and timing of these demands are complicated in marine-adapted mammals by the involvement of the dive response during underwater exercise (discussed in the following section) and by the need for rapid post-dive recovery of tissue oxygen stores between dives as the animals briefly surface to breathe (9, 30, 44). This unique respiratory-cardiovascular timing dictates the species-specific mass of cetacean and pinniped hearts (FIGURE 1B).

For mammals that inhabit the seas, the size of the heart falls into two categories: 1) the pinnipeds (seals and sea lions), sea otter, and small odontocetes (toothed whales such as dolphins and porpoises, including the killer whales Orcinus orca), and 2) the great whales (mysticete whales and sperm whales that exceed 10,000 kg). Here, the distinction in heart size appears to follow the propensity of individual species for high-speed swimming, especially near the water surface, and the associated management of oxygen-carrying globins that transit between or reside within the tissues (60). The pinniped and dolphin group includes the more athletic species that surf, leap, and perform rapid maneuvers when chasing prey. The heart size of these marine mammals averages $0.90 \pm 0.06\%$ of body mass ($n = 9$ across 6 species), which follows the trend of their wild aerobic mammal ancestors (FIGURE 1) as well as extant semi-aquatic carnivores such as minks and otters. In contrast, the average heart size of the great whales is $0.52 \pm 0.05\%$ of body mass ($n = 5$ across 3 species), 13% smaller than predicted. Because of the difficulty in obtaining such measurements and in determining $\dot{V}O_{2max}$ for these large, oceanic mammals, it is premature to speculate about the effect of heart size on aerobic capacity for the great whales. However, one could argue that the mechanical and biochemical challenges associated with coordinating the beat of a heart that can exceed 200 kg in mysticete whales and sperm whales may limit the ultimate size of this organ (FIGURE 1B) and its proportion to body mass. Consequently, one study on a 43,000-kg sperm whale reported a heart mass of 138 kg (37) that was only 0.32% of body mass, half the predicted size based on other mammals. At the other extreme, the smallest mammal in our review, the Etruscan shrew, has a heart that is nearly double the predicted size based on body mass, presumably to circumvent mechanical limitations in heart-beat frequency that can reach 1,500 beats/min during exercise (18). Clearly, heart size and function are modified to meet the demands of extreme size in mammals.

## Conflict Resolution in the Exercising Heart

The diversity of mammalian species and their remarkable range in body size, lifestyles, and hunting strategies provide unique opportunities for examining the capacity of the mammalian heart to function under extreme conditions. By demonstrating the limits of organ function, such comparative studies also improve our ability to predict when demands placed on the human heart may exceed performance capabilities. Nowhere has this been more evident than when the cardiovascular responses of diving humans and marine mammals are examined (30).

For the past two decades, scientists have debated how marine mammals such as seals and dolphins are able to balance cardiovascular demands when exercising underwater (9, 10, 14, 15), especially since humans are so poorly adapted for these conditions (6, 28, 49). The paradox stems from two ancient and seemingly conflicting physiological responses that occur when a mammal submerges (FIGURE 2; Ref. 57). The dive response is characterized by the cessation of breathing (apnea), a slowing of the heart (bradycardia), and peripheral vasoconstriction while maintaining aerobic metabolic and physiological function in most tissues and organs (14). Conversely, the mammalian exercise response promotes an increase in metabolism, heart rate (tachycardia), and respiratory rate. For an active diving mammal, these responses must be integrated from the level of the myocardial cells (12) to the whole animal. Thus, as with human divers (20, 42), the heart rate of marine mammals is the dynamic net result of inputs from baroreceptors (1), pulmonary stretch receptors (2), blood gases (44), cardiovascular hormones (e.g., natriuretic peptides; Ref. 53), and more. Changes in hydrostatic pressure as the diver moves through the water column result in an additional input, with physical compression and expansion of the lungs and pulmonary shunting affecting heart rate during descent and ascent (20, 21). In view of this complexity and frequently opposing inputs, how does a diving mammal maintain cardiac stability?

Recently, we developed a miniaturized electrocardiographic recorder coupled with a depth sensor and three-axis accelerometer (ECG-ACC recorder) to provide detailed insight into the

responses of the mammalian heart to underwater exercise (15, 41, 57). Using this instrument, we have found that the cardiovascular response of seals and dolphins is less of a simple democratic averaging of the various cardiac inputs and more of a rapid alternating exchange between dominating factors (FIGURE 3). A similar exchange appears to occur in humans when exercise is combined with submersion (49).

Rather than a single level of bradycardia, heart rate in marine-adapted mammals is influenced by both the level of exercise and the depth where exercise takes place (FIGURE 3A). For example, the lowest heart rates occur on the deepest dives of California sea lions (*Zalophus californianus*; Ref. 38), Weddell seals (*Leptonychotes weddellii*), and bottlenose dolphins (*Tursiops truncatus*; Ref. 57). As swimming exercise intensifies (e.g., when chasing fish), a normal increase in heart rate associated with the level of physical exertion is superimposed on the diving bradycardia. Consequently, periods

of high stroke frequency are associated with a relaxation in bradycardia (and elevated heart rates), whereas low stroke frequency swimming or gliding is associated with more intense bradycardia (and the lowest heart rates). Whatever the level of exertion or depth, heart rate is adjusted to optimize the consumption of oxygen stored in the lungs, blood, and muscles to maximize dive duration (FIGURE 3A; Ref. 13).

Analogous patterns in cardiac variability while submerged have been demonstrated for human breath-hold divers (6, 28) and attributed to the interplay between opposing sympathetic and parasympathetic neural drivers that control exercise and diving responses, respectively (FIGURE 3, A AND B; Refs. 21, 33). As might be expected, normal cardiac rhythms can be compromised when these cardiac-stimulating and -suppressing neural signals interfere or switch quickly. Termed an "autonomic conflict" by Shattock and Tipton (49), simultaneous
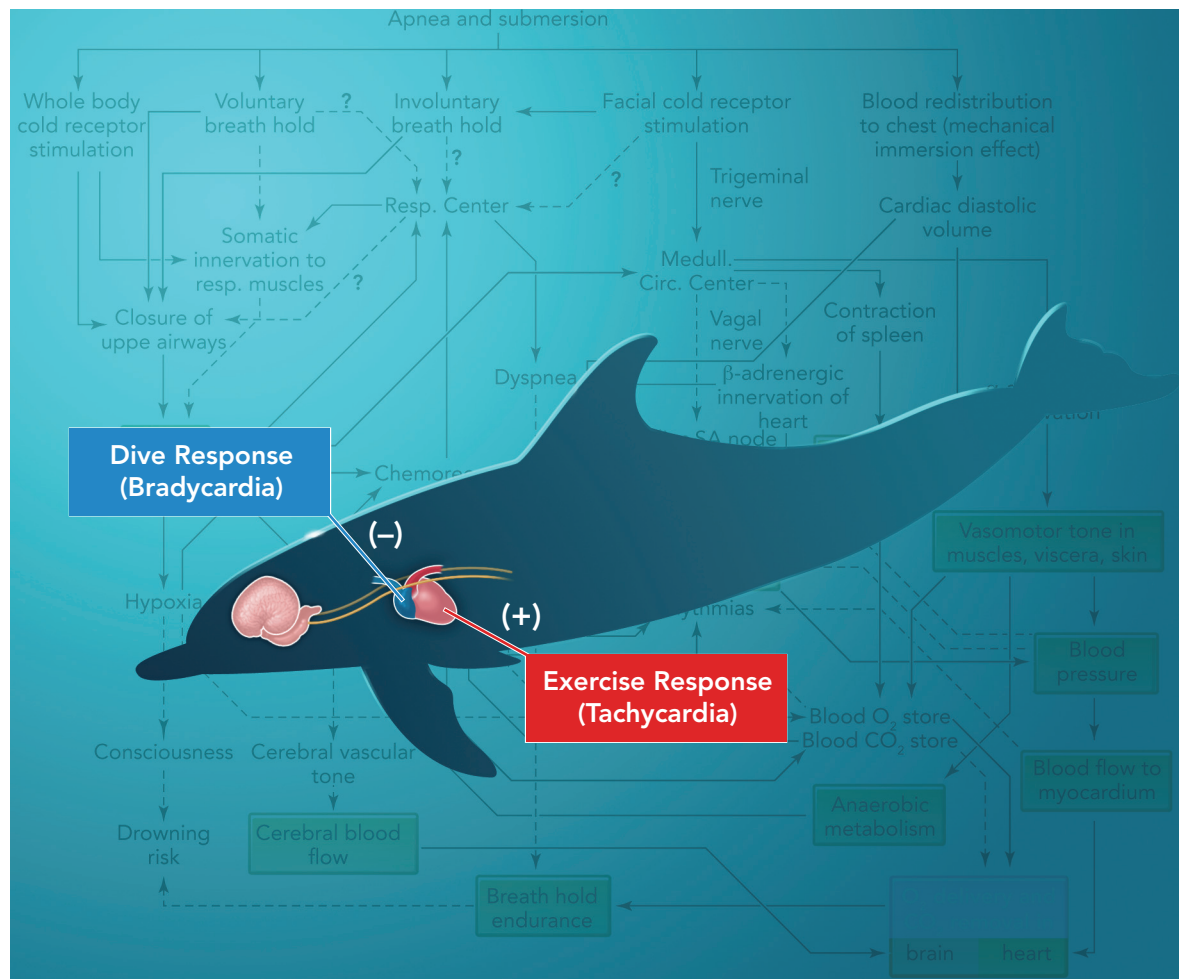


**FIGURE 2. Physiological control of the heart of a diving dolphin**
The background of the illustration indicates some of the complex interactions that dictate heart rate during a dive; exercise adds another layer of control when the animal is actively swimming. Background was based on data from Ref. 20. For the diving dolphin, opposing neural signals associated with the dive response (blue box) and exercise response (red box) result in simultaneous negative and positive drivers controlling heart rate, respectively.

antagonistic signals from a sympathetically controlled cold shock response and the parasympathetically controlled diving response induce cardiac arrhythmias in healthy humans submersed in cold water. When combined with predisposing cardiac conditions such as atherosclerosis, myocardial hypertrophy, ischemic heart disease, or heritable long QT syndrome, these arrhythmias may be lethal. The investigators concluded that such a combination of factors may serve as an underappreciated cause of death in immersion-related accidents in humans (49). Considering the combination of intense exercise demands and abrupt immersion, perhaps it is not surprising that the swimming segment of triathlons accounts for over 90% of race day deaths (25), especially in cold water venues.

Despite adaptations for underwater activity and prolonged submergence, diving marine mammals also display a surprisingly high incidence of cardiac arrhythmias. Our ECG-ACC monitors revealed that the quick transitions between short periods of tachycardia and bradycardia (FIGURE 3B) that occurred with high-intensity swimming promoted
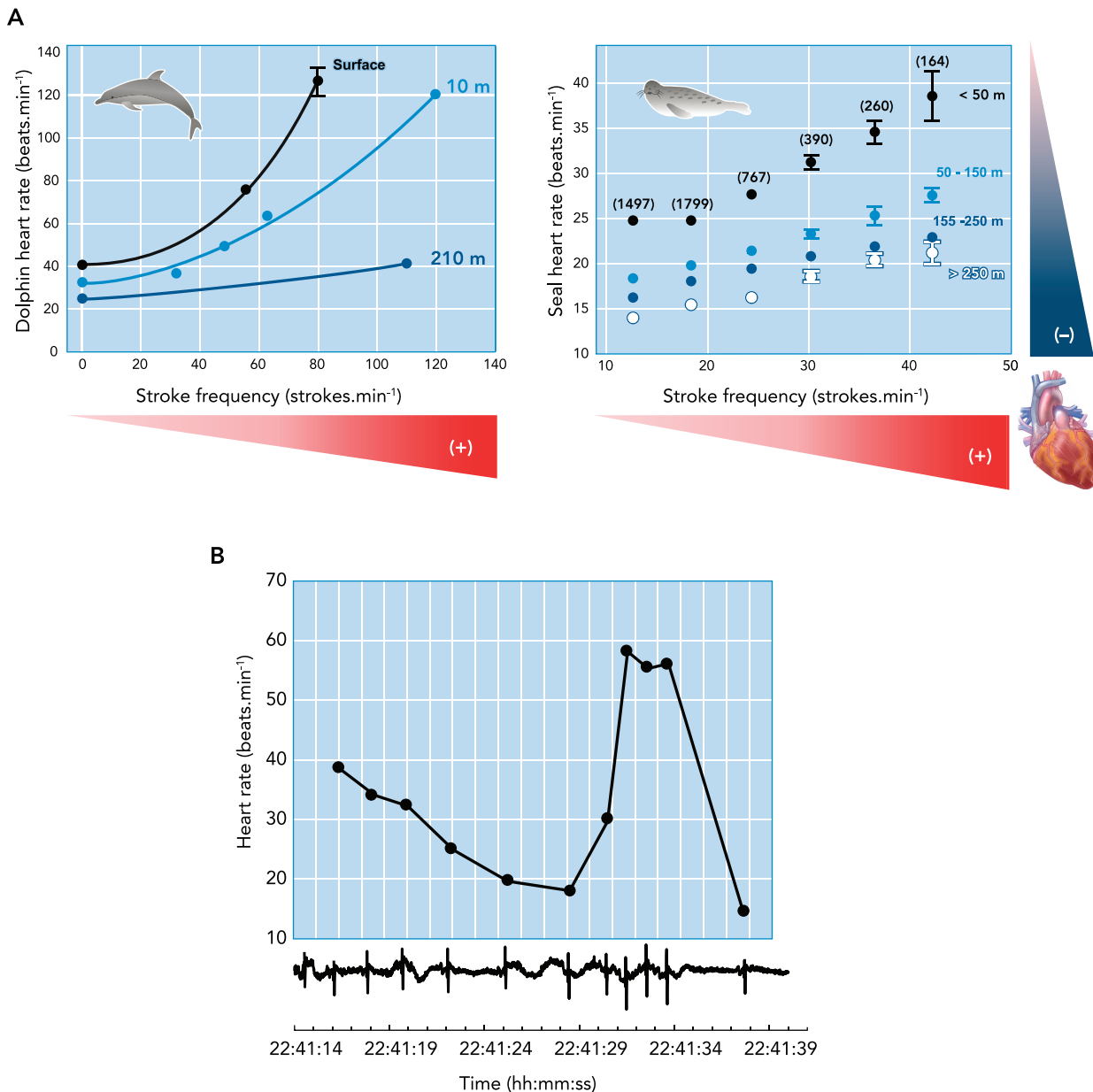


FIGURE 3. **Variability in heart rate during diving by bottlenose dolphins and Weddell seals**
A: the change in heart rate due to swimming stroke frequency and depth. Symbols represent mean heart rate at instantaneous depths, which range from near the surface (black) to the deepest depths measured for dolphins (cyan, 210 m) and seals (white, >250 m). Numbers in parentheses show the total number of heart-rate intervals measured for each depth, with $n = 344$ for the dolphins. Bordering triangles denote hypothetical grade changes in the parasympathetic diving response (blue) and sympathetic exercise response (red), representing the major neural drivers for heart rate. Symbols and vertical or horizontal lines show means ± SE. B: a typical ECG trace and corresponding heart rate for a diving Weddell seal. Note the rapid exchange between bradycardia and tachycardia over the 25-s period at depth.

an increase in the incidence of ectopic heart beats in seals and dolphins, especially during deep dives (57). Over 73% of deep dives to ~290 m ($n = 26$) by Weddell seals involved some form of cardiac arrhythmia. This compares with only 26% of shallow dives to <100 m ($n = 19$) displaying ectopic beats. An identical pattern was observed for open-ocean trained bottlenose dolphins. For the cetaceans, over 81% of dives to 210 m ($n = 11$) showed high levels of cardiac variability and arrhythmic periods during ascent compared with 8% of dives to 60 m ($n = 13$). For both species, arrhythmias were most likely to occur during periods of intense stroking at the initiation of directed ascents from depth.

Importantly, by modifying the rate of ascent or descent, and switching from constant stroking to interrupted modes of propulsion (i.e., burst-and-glide swimming), marine mammals were able to behaviorally control periods of cardiac instability and perform deep-sea chases without incident (57). In view of this, how important is conscious control of heart rate via behavior for ensuring heart health in mammals?

## Extreme Exercise: Where Heart and Head Integrate

Ultimately, master control of the heart comes from the central nervous system (20). Yet, relative to the decades of study on cellular, physiological, and environmental factors affecting cardiac function, we are just beginning to appreciate this higher psychological level of cardiac integration in wild animals and humans athletes (5). The implications are both fascinating and profound.

As noted above, conscious control of heart rate through behavioral modification appears to be an effective mechanism for maintaining cardiac stability in extreme diving mammals. To determine just how well these mammals can control bradycardia, Ridgway and colleagues (45) conducted an elegent experiment in which a California sea lion (*Zalophus californianus*) was trained through operant conditioning to reduce its heart rate on command while sitting in air. The lowest heart rate achieved by the trained animal was 10 beats/min, far exceeding the level of bradycardia reached through a parasympathetic nervous reflex when the sea lion voluntarily immersed its head in a bucket of water. Similarly, during our experiments with diving dolphins (41), trainers recalling an animal from an ascent and back to depth could initiate an abrupt interruption of the pre-surface tachycardia to a reinstatement of diving bradycardia. These tests, together with observations of wild animals, suggest that marine mammals are capable of considerable conscious modification of the level of diving bradycardia, perhaps even setting heart rate in anticipation of the length of submergence or to avoid arrhythmias. In this regard, the damping of
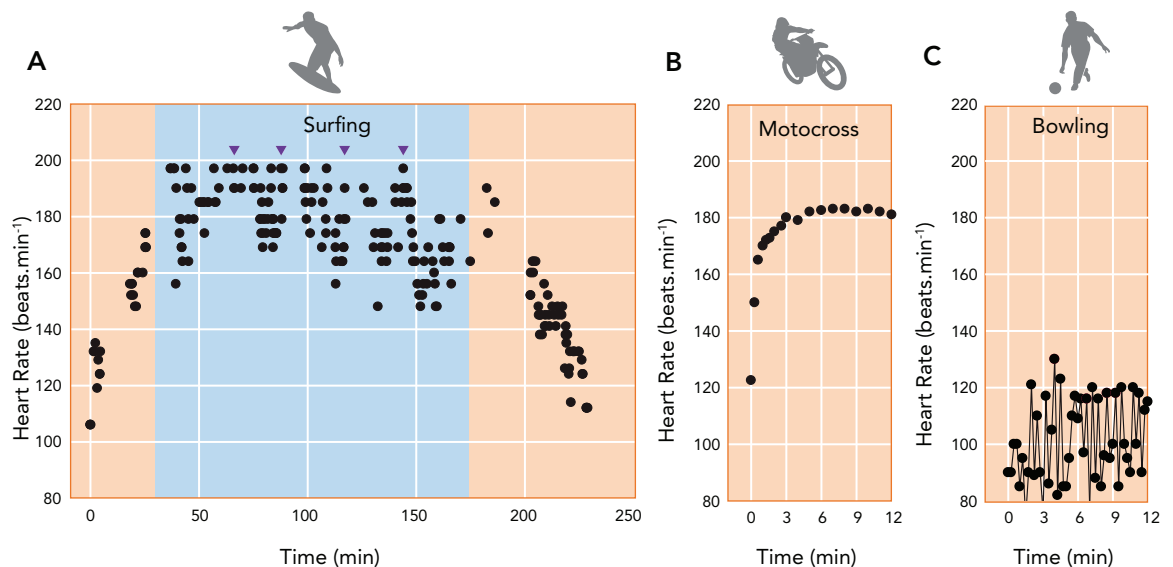


FIGURE 4. **The effect of extreme and routine sports on heart rate in human competitors**
Values for heart rate in relation to time are compared for extreme surfing by a professional male surfer on 7- to 10-m waves (*A*), a male motocross racer (*B*), and a male novice bowler (*C*). For the surfer, the changes in heart rate on the beach before and after competition (tan background) and time in the wave zone (blue background) are shown. Black circles represent the average heart rate for 5-s periods during a representative surfing session lasting 4 h. Triangles indicate periods when the subject was wave-riding. *B*: data is from Konttinen et al. (29) for motocross competitors riding on an outdoor track. Each circle represents the average heart rate across 20 s. *C*: the circles denote heart-rate measurements at 30-s intervals. Peak values correspond to hitting the pins, whereas the lowest values are for the resting interval between throws. Despite differences in the intensity of the sport, all competitors demonstrated a sympathetically driven thrill response on heart rate superimposed on the physical exercise response.

heart rate via central control by diving mammals has been likened to that of meditating yogis (19).

At the opposite end of the heart-rate spectrum, extreme athletes can also consciously affect heart function by placing continuous, high-level demands on the cardiovascular system through progressive thrill-seeking behaviors (5, 40). In addition to physical work, athletes participating in high-risk and extreme sports such as hang-gliding, auto racing, BMX biking, and mountain/rock climbing are challenged by prolonged mental stress due to the risk inherent in such sports. Under these conditions, higher central nervous control can override the normal autonomic response to exercise by the heart.

We investigated the relative effect of physical exercise and psychological thrill-seeking responses on cardiac function in athletes by deploying heart rate monitors on participants of an extreme sport, big-wave surfing (55). While the instrumented athletes surfed on waves that ranged in height from 1- to 10-m swells, observers on land recorded continuous behavioral data on the timing and details of in-water activities (paddling to site, paddling into waves, surfing waves, and inter-wave submergence). We discovered that professional surfers, when actively riding a wave, maintained exceptionally high heart-rate levels that were ~90% of maximal heart rate ($HR_{max}$) determined during treadmill running. Unexpectedly, these near maximum heart rates occurred whether the wave face was a moderate 1–3 m or an extreme 7–10 m in height. For these athletes, sympathetically driven thrill seeking behavior rather than the level of physical exertion dictated heart rate. This psychological override resulted in one of the highest, prolonged heart rate levels (182.0 ± 1.1 beats/min during 3 h of extreme surfing) measured for an endurance activity (FIGURE 4A). In comparison, mean heart rates of 70% $HR_{max}$ have been measured for endurance bicyclists participating in the Tour de France (34, 35). To date, only motocross racers (a cross-county, open-terrain motorcycle event; FIGURE 4B) and Formula racing car drivers have been found to maintain 90% $HR_{max}$ levels of professional surfers but for much shorter (e.g., 40–50 min) competitive events (29, 48).

Because they bypass the adaptive reductions in energetic demands (56) and cardiovascular reactivity to psychological stress (6, 50) that represent common benefits of aerobic exercise training and experience, extreme athletes incur a cardiovascular cost in thrill-seeking. Even bowlers can experience the adrenaline surge of competition with a 50% spike in heart rate in anticipation of a strike or simply hitting a pin, albeit at an overall lower level of heart rate compared with extreme athletes (FIGURE 4C). Such seemingly wasteful physiologi-

**Table 1.** *2015 American Heart Association recommendations for heart health (39)*

| For Overall Cardiovascular Health Engage in One of the Following |
| --- |
| ● A minimum of 25 min of vigorous aerobic activity at least 3 days/wk for a total of 75 min |
| ● A minimum of 25 min of vigorous aerobic activity at least 3 days/wk for a total of 75 min |
| ● A combination of moderate- and vigorous-intensity aerobic activity with moderate- to high-intensity muscle strengthening activity at least 2 days/wk for additional health benefits |

| To Lower Blood Pressure and Cholesterol Engage in |
| --- |
| ● An average of 40 min of moderate- to vigorous-intensity aerobic activity 3 or 4 times/wk |

cal costs are usually avoided by wild animals striving to maintain daily energetic balance for survival. Thus we find that, while surfing elicits maximum heart rates in extreme athletes (FIGURE 4A), dolphins display the opposite pattern, with reduced heart rates and energetics costs when catching a wave (56). For the animals, the benefit of surfing was in obtaining an inexpensive ride down the wave rather than a psychological thrill.

## Conclusions

Taking a comparative approach to evaluate the response of the mammalian heart to unique physical and psychological challenges has provided new insights into the functional limits of this organ. For example, in marine mammals, the suite of behaviors contributing to cardiac anomalies when submerged (elevated levels of physical exertion, deep diving, rapid ascent from depth; Ref. 57) are identical to those displayed during the flight responses of whales exposed to shipping noise and mid-frequency sonars (16, 23). Because these responses may override natural behavioral safeguards for maintaining cardiac stability when diving, monitoring these behaviors and related cardiac responses provides a new method for ensuring heart health in oceanic mammals exposed to anthropogenic disturbances.

These new findings on autonomic conflicts in the hearts of swimmers and divers have also benefitted the human athlete. USA Triathlon (USAT), the national governing body for triathlon race events, has recently undertaken a comprehensive study of fatalities and sudden cardiac death in swimmers. Non-traumatic (accident related) fatalities occur in triathlons at a rate of ~1 in every 76,000 participants overall, with the swim portion consistently the major contributor. The swimming portion of the race was responsible for 35 of 43 deaths in triathlons during the period of 2002–2012. Currently, no specific correlation between

the experience of the athlete, the distance of the race, ocean vs. lake venues, or the method of the swim start (wave start, mass start, time trial) and death has been identified. However, with cold water and the stress of competition as potential contributing factors to autonomic conflicts in swimmers (42, 49), USAT is now evaluating the thermic effect of competition in very cold or very hot water. The goal is to further understand the links between the physical, psychological, and environmental challenges to the athlete's heart, and to set guidelines for triathlon swims within safe physiological limits.

In general, we have found that the mammalian heart is remarkably resilient under extreme conditions as well as during intense physical and psychological demands. Based on morphology and response to training, the human heart is especially adapted for aerobic performance that rivals that of other athletic mammals (FIGURE 1). Unfortunately, the majority of humans of all ages clearly underutilize this amazing organ through a lifelong habit of sedentary living that has contributed to an extraordinary high incidence of cardiovascular disease (39).

For wild mammals as well as our human ancestors (32), a large proportion of the day was usually spent grazing or locating, chasing, killing, and consuming prey. For example, marine mammals such as Weddell seals (*Leptonychotes weddellii*) and sea otters (*Enhydra lutris*) spend 40–60% of the day active (59). On land, even the most lethargic mammalian carnivores, as exemplified by the African lion (*Panthera leo*), average 4–8 h/day hunting (26, 47). Furthermore, an active lifestyle begins early in young wild mammals; for dolphins and whales, it begins at the moment of birth as soon as the neonate enters the water and swims to the surface for its first breath. By comparison, <37% of children meet the minimum American Heart Association recommendation of 75–160 min of activity per week. The statistic for human adults is worse, with <45% of the adult population meeting this minimum (Table 1; Ref. 39). Large, wild mammals accomplish these recommended weekly exercise levels in one daily hunting trip.

For the less athletically inclined individuals among us, these studies on wild mammals and extreme athletes should inspire a heightened awareness of the importance of a natural level of daily activity for heart health. Given the longevity and cardiac health of many species of wild mammals, perhaps it is time for humans to adopt a wilder daily exercise plan. ∎

## References

1. Angell-James JE, deBurgh Daly M, Elsner R. Arterial baroreceptor reflexes in the seal and their modification during experimental dives. *Am J Physiol Heart Circ Physiol* 234: H730–H739, 1978.

2. Angell-James JE, Elsner R, deBurgh Daly M. Lung inflation: effects on heart rate, respiration, and vagal afferent activity in seals. *Am J Physiol Heart Circ Physiol* 240: H190–H198, 1981.

3. Bishop CM. The maximum oxygen consumption and aerobic scope of birds and mammals: getting to the heart of the matter. *Proc R Soc Lond B* 266: 2275–2281, 1999.

4. Bonnett BN, Egenvall A. Age patterns of disease and death in insured swedish dogs, cats and horses. *J Comp Pathol* 142: S33–S38, 2010.

5. Breivik G, Roth WT, Jørgensen PE. Personality, psychological states and heart rate in novice and expert parachutists. *Personality Individual Differences* 25: 365–380, 1998.

6. Breskovic T, Uglesic L, Zubin P, Kuch B, Kraljevic J, Zanchi J, Ljubkovic M, Sieber A, Dujic Z. Cardiovascular changes during underwater static and dynamic breath-hold dives in trained divers. *J Appl Physiol* 111: 673–678, 2011.

7. Brody S. *Bioenergetics and Growth with Special Reference to the Efficiency Complex in Domestic Animals*. New York: Reinhold Publishing, 1945.

8. Brooks G, Fahey T, Baldwin K. *Exercise Physiology: Human Bioenergetics and Its Applications*. New York: McGraw-Hill Humanities, 2004.

9. Butler PJ, Jones J. Physiology of diving of birds and mammals. *Physiol Rev* 77: 837–899, 1997.

10. Castellini MA, Murphy BJ, Fedak M, Ronald K, Gofton N, Hochachka PW. Potentially conflicting metabolic demands of diving and exercise in seals. *J Appl Physiol* 58: 392–399, 1985.

11. Chassin PS, Taylor CR, Heglund NC, Seeherman HJ. Locomotion in lions: energetic cost and maximum aerobic capacity. *Physiol Zool* 49: 1–10, 1976.

12. Daniels S, Grossman Y. Biological effects of pressure. In: *Physiology and Medicine of Diving* (5th ed.), edited by Brubakk AO, Neuman TS. New York: Saunders, 2003, p. 265–299.

13. Davis RW, Kanatous SB. Convective oxygen transport and tissue oxygen consumption in Weddell seals during aerobic dives. *J Exp Biol* 202: 1091–1113, 1999.

14. Davis RW, Polasek L, Watson R, Fuson A, Williams TM, Kanatous SB. The diving paradox: new insights into the role of the dive response in air-breathing vertebrates. *Comp Biochem Physiol A* 138: 263–268, 2004.

15. Davis RW, Williams TM. The marine mammal dive response is exercise modulated to maximize aerobic dive duration. *J Comp Physiol A* 198: 583–591, 2012.

16. DeRuiter SL, Southall BL, Calambokidis J, Zimmer WM, Sadykova D, Falcone EA, Friedlaender AS, Joseph JE, Moretti D, Schorr GS, Thomas L, Tyack PL. First direct measurements of behavioural responses by Cuvier's beaked whales to mid-frequency active sonar. *Biol Lett* 9: 20130223, 2013.

17. Dill DB. Marathoner DeMar: physiological studies. *J Natl Cancer Inst* 35: 185–191, 1965.

18. Dobson GP. On being the right size: heart design, mitochondrial efficiency and lifespan potential. *Clin Exp Pharm Physiol* 30: 590–597, 2003.

19. Elsner R. *Diving Seals and Meditating Yogis: Strategic Metabolic Retreats.* Univ. of Chicago Press, 191pp, 2015.

20. Ferrigno MF, Lundgren CE. Breath-hold diving. In: *Physiology and Medicine of Diving* (5th ed.), edited by Brubakk AO, Neuman TS. New York: Saunders, 2003, p. 153–180.

21. Foster GE, Sheel AW. The human dive response, its function, and its control. *Scand J Med Sci Sports* 15: 3–12, 2005.

22. George JC, Bada J, Zeh J, Scott L, Brown SE, O'Hara T, Suydam R. Age and growth estimates of bowhead whales (*Balaena mysticetus*) via aspartic acid racemization. *Can J Zool* 77: 571–580, 1999.

23. Goldbogen JA, Southall BL, DeRuiter SL, Calambokidis J, Friedlaender AS, Hazen EL, Falcone EA, Schorr GS, Douglas A, Moretti DJ, Kyburg C, McKenna MF, Tyack PL. Blue whales respond to simulated mid-frequency military sonar. *Proc R Soc B* 280: 20130657, 2013.

24. Gunn HM. Heart weight and running ability. *J Anat* 167: 225–233, 1989.

25. Harris KM, Henry JT, Robman E, Haas TS, Maron BJ. Sudden death during the triathlon. *JAMA* 303: 1255–1257, 2010.

26. Hayward MW, Slotow R. Temporal partitioning of activity in large african carnivores: tests of multiple hypotheses. *South African J Wildlife Res* 39: 109–125, 2009.

27. Hoppeler H, Lindstedt SL, Claasen H, Taylor CR, Mathieu O, Weibel ER. Scaling mitochondrial volume in heart to body mass. *Respir Physiol* 55: 131–137, 1984.

28. Kiviniemi AM, Breskovic T, Uglesic L, Kuch B, Maslov PZ, Sieber A, Seppänen T, Tulppo MP, Dujic Z. Heart rate variability during static and dynamic breath-hold dives in elite divers. *Auton Neurosci* 169: 95–101, 2012.

29. Konttinen T, Häkkinen K, Kyröläinen H. Cardiopulmonary loading in motocross riding. *J Sports Sci* 25: 995–999, 2007.

30. Kooyman GL. *Diverse Divers: Physiology and Behavior.* Berlin: Springer-Verlag, 1989.

31. Kreuder C, Miller MA, Jessup DA, Lowenstine LJ, Harris MD, Ames JA, Carpenter TE, Conrad PA, Mazet JAK. Patterns of mortality in southern sea otters (*Enhydra lutris nereis*) from 1998–2001. *J Wildl Dis* 39: 495–509, 2003.

32. Leonard WR. Size counts: evolutionary perspectives on physical activity and body size from early hominids to modern humans. *J Physical Activity Health* 7, Suppl 3: S284–S298, 2010.

33. Levy MN. Brief reviews: sympathetic-parasympathetic interactions in the heart. *Circ Res* 29: 437–445, 1971.

34. Lucia A, Hoyos J, Carvajal A, Chicharro JL. Heart rate response to professional road cycling: the Tour de France. *Int J Sports Med* 20: 167–172, 1999.

35. Lucia A, Hoyos J, Santalla A, Earnest C, Chicharro JL. Tour de France versus Vuelta a Espana: which is harder? *Med Sci Sports Exerc* 35: 872–878, 2003.

36. Mazak V. *Panthera tigris. Mammalian Species* 152: 1–8, 1981.

37. McAlpine DF. Size and growth of heart, liver, and kidneys in North Atlantic fin (*Balaenoptera physalus*), sei (*B. borealis*), and sperm (*Physeter macrocephalus*) whales. *Can J Zool* 63: 1402–1409, 1985.

38. McDonald BI, Ponganis PJ. Deep-diving sea lions exhibit extreme bradycardia in long-duration dives. *J Exp Biol* 217: 1525–1534, 2014.

39. Mozaffarian, et al. D. Heart disease and stroke statistics: 2015 update: a report from the American Heart Association. *Circulation* 131: e29–e322, 2015.

40. Murray DM. *Living on the Edge: Sensation Seeking and Extreme Sports Participation* (PhD thesis). Storrs, CT: Univ. Connecticut, 2003.

41. Noren SR, Kendall T, Cuccurullo V, Williams TM. The dive response redefined: underwater behavior influences cardiac variability in freely diving dolphins. *J Exp Biol* 215: 2735–2741, 2012.

42. Olsen CR, Fanestil DD, Scholander PF. Some effects of breath holding and apneic underwater diving on cardiac rhythm in man. *J Appl Physiol* 17: 461–466, 1962.

43. O'Neill DG, Church DB, McGreevy PD, Thomson PC, Brodbelt DC. Longevity and mortality of cats attending primary care veterinary practices in England. *Vet J* 198: 638–643, 2013.

44. Ponganis PJ, Kooyman GL, Ridgway SH. Comparative diving physiology. In: *Physiology and Medicine of Diving* (5th ed.), edited by Brubakk AO, Neuman TS. New York: Saunders, 2003, p. 211–226.

45. Ridgway SH, Carder DA, Clark W. Conditioned bradycardia in the sea lion, *Zalophus californianus. Nature* 256: 37–38, 1975.

46. Roelke ME, Martenson JS, O'Brien SJ. The consequences of demographic reduction and genetic depletion in the endangered Florida panther. *Curr Biol* 3: 340–350, 1993.

47. Schaller GB. *The Serengeti Lion: A Study of Predator-Prey Relations.* Chicago, IL: Univ. of Chicago Press, 1972.

48. Schwaberger G. Heart rate, metabolic and hormonal responses to maximal psycho-emotional and physical stress in motor car racing drivers. *Int Arch Occup Environ Health* 59: 579–604, 1987.

49. Shattock MJ, Tipton MJ. "Autonomic Conflict": a different way to die during cold water immersion? *J Physiol* 590: 3219–3230, 2012.

50. Spalding TW, Lyon LA, Steel DH, Hatfield BD. Aerobic exercise training and cardiovascular reactivity to psychological stress in sedentary young normotensive men and women. *Psychophysiology* 41: 552–562, 2004.

51. Stahl WR. Organ weights in promotes and other mammals. *Science* 150: 1039–1042, 1965.

52. Stahl WR. Scaling of respiratory variables in mammals. *J Appl Physiol* 22: 453–460, 1967.

53. Tota B, Cerra MC, Gattuso A. Catecholamines, cardiac natriuretic peptides and chromogranin A: evolution and physiopathology of a 'whip-brake' system of the endocrine heart. *J Exp Biol* 213: 3081–3103, 2010.

54. Weibel ER, Bacigalupe LD, Schmitt B, Hoppeler H. Allometric scaling of maximal metabolic rate in mammals: muscle aerobic capacity as determinant factor. *Respir Physiol Neurobiol* 140: 115–132, 2004.

55. Williams TM. The physiology of surfing. In: *53rd Annual Meeting of the American College of Sports Medicine, May 31-June 3, Denver CO, 2006.* Denver, CO: Am. Coll. of Sports Medicine, 2006.

56. Williams TM, Friedl WA, Fong ML, Yamada R, Sedivy P, Haun JE. Travel at low energetic cost by swimming and wave-riding bottlenose dolphins. *Nature* 355: 821–823, 1992.

57. Williams TM, Fuiman LA, Kendall T, Berry P, Thometz N, Richter B, Noren SR, Shattock MJ, Farrell E, Stamper AM, Davis RW. Exercise at depth alters bradycardia and incidence of cardiac anomies in deep-diving marine mammals. *Nat Commun* 6: 6055, 2015.

58. Williams TM, Wolfe L, Davis T, Kendall T, Richter B, Wang Y, Bryce C, Elkaim G, Wilmers CC. Instantaneous energetics of puma kills reveal advantage of felid sneak attacks. *Science* 346: 81–85, 2014.

59. Williams TM, Yeates L. The energetics of foraging in large mammals: a comparison of marine and terrestrial predators. *Intl Congress Series* 1275: 351–358, 2004.

60. Williams TM, Zavanelli M, Miller MA, Goldbeck RA, Morledge M, Casper D, Pabst DA, McLellan W, Cantin LP, Kliger DS. Running, swimming and diving modifies neuroprotecting globins in the mammalian brain. *Proc R Soc Lond* B 275: 751–758, 2008.