PHILOSOPHICAL
TRANSACTIONS B

royalsocietypublishing.org/journal/rstb

Introduction

Cite this article: Hawkes LA, Fahlman A, Sato K. 2021 Introduction to the theme issue: Measuring physiology in free-living animals. *Phil. Trans. R. Soc. B* **376**: 20200210.
https://doi.org/10.1098/rstb.2020.0210

Accepted: 19 April 2021

One contribution of 10 to a theme issue 'Measuring physiology in free-living animals (Part I)'.

Subject Areas:
bioengineering, ecology, environmental science, health and disease and epidemiology, physiology

Keywords:
biologging, nanosensor, electronic engineering, medicine, diving, flight

Author for correspondence:
L. A. Hawkes
e-mail: l.hawkes@exeter.ac.uk

Introduction to the theme issue: Measuring physiology in free-living animals

L. A. Hawkes[1], A. Fahlman[2,3] and K. Sato[4]

[1]Hatherly Laboratories, University of Exeter, Prince of Wales Road Exeter EX4 4PS, UK
[2]Global Diving Research Inc, Ottawa, Ontario, Canada
[3]Fundación Oceanogràfic de la Comunitat Valencia, Valencia, 46005 Spain
[4]Atmosphere and Ocean Research Institute, University of Tokyo, 5-1-5 Kashiwanoha, Kashiwa, Chiba Prefecture 277-8564, Japan

LAH, 0000-0002-6696-1862; AF, 0000-0002-8675-6479; KS, 0000-0002-7557-4784

By describing *where* animals go, biologging technologies (i.e. animal attached logging of biological variables with small electronic devices) have been used to document the remarkable athletic feats of wild animals since the 1940s. The rapid development and miniaturization of physiologging (i.e. logging of physiological variables such as heart rate, blood oxygen content, lactate, breathing frequency and tidal volume on devices attached to animals) technologies in recent times (e.g. devices that weigh less than 2 g mass that can measure electrical biopotentials for days to weeks) has provided astonishing insights into the physiology of free-living animals to document *how* and *why* wild animals undertake these extreme feats. Now, physiologging, which was traditionally hindered by technological limitations, device size, ethics and logistics, is poised to benefit enormously from the on-going developments in biomedical and sports wearables technologies. Such technologies are already improving animal welfare and yield in agriculture and aquaculture, but may also reveal future pathways for therapeutic interventions in human health by shedding light on the physiological mechanisms with which free-living animals undertake some of the most extreme and impressive performances on earth.

This article is part of the theme issue 'Measuring physiology in free-living animals (Part I)'.

1. Introduction

The field of 'biologging' (i.e. animal attached logging of biological variables with small electronic devices) has revealed how species of wild animals undertake remarkable feats of athleticism that set the benchmark for vertebrate performance. In the aerial environment, this includes non-stop endurance migratory flights of over 11 000 km by bar-tailed godwits (*Limosa lapponica* [1]), extreme long-distance migrations of more than 100 000 km by Arctic terns (*Sterna paradisaea* [2]), high-altitude flights of over 6000 m altitude by bar-headed geese (*Anser indicus* [3–6]) and non-stop flights for more than 10 months of the year by common swifts (*Apus apus* [7]). Similar remarkable feats have been recorded in the aquatic realm, including dives beyond 500 m deep by emperor penguins (*Aptenodytes forsteri* [8]), dives beyond 2 km deep by elephant seals (*Mirounga* sp.) resulting in near total venous blood oxygen depletion [9–11] and dives to nearly 3 km deep [12] for over 3 h [13] by Cuvier's beaked whales (*Ziphius cavirostris*). These astonishing feats highlight the fact that not only is it important to conserve wildlife for aesthetic and ethical reasons [14], but also because these athletic species may help to highlight medical pathways and approaches for some of the greatest health challenges for humans, including hypoxia (e.g. strokes and heart attacks), diabetes and obesity. The inspiration for this theme issue came from animal biologists attending conferences of Extreme and Expedition

THE ROYAL SOCIETY
PUBLISHING

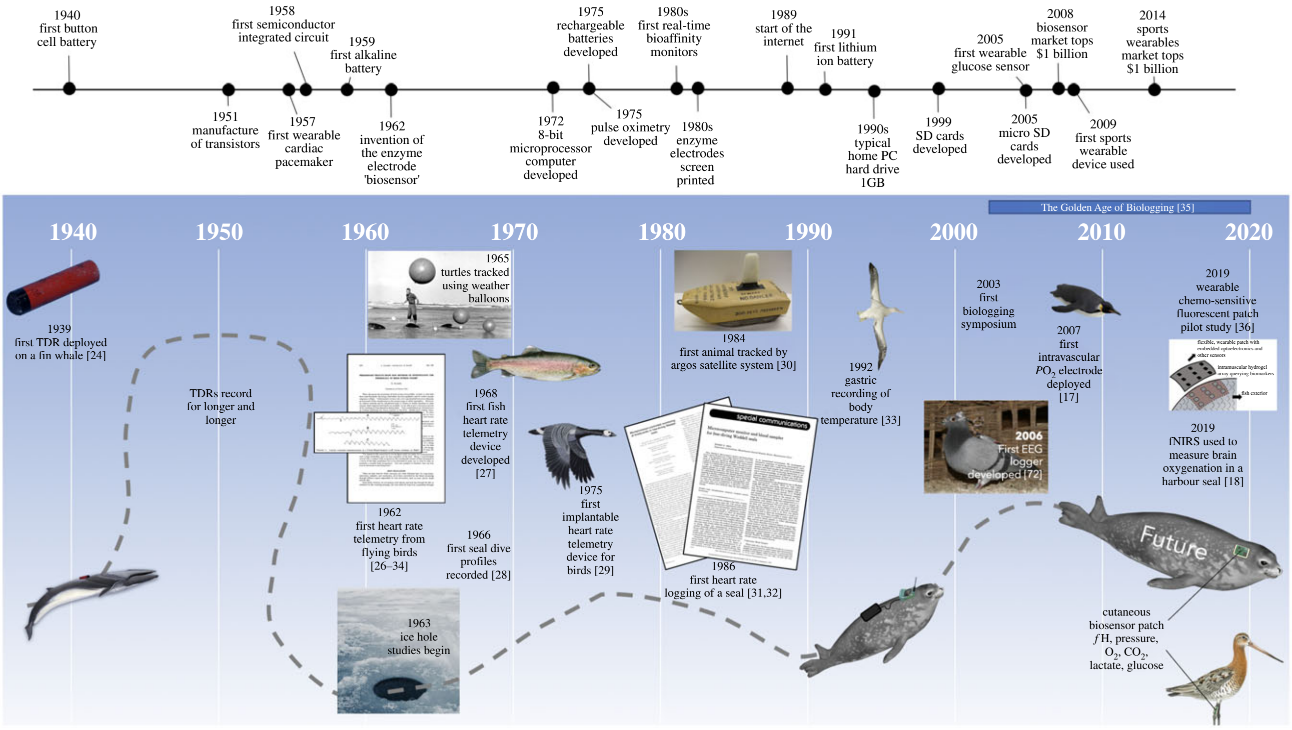

Figure 1. Timeline of (top) electronic and microprocessor development from the 1940s to the present day; and (bottom) key events in the field of physiologging. (Online version in colour.)

Medics, where researchers were engaged in medical studies in similar ecosystems (e.g. high altitude, [15,16]). While a few recent studies have made use of medical technologies designed for humans to study the diving capacity of humans and seals [17,18], medical studies generally have access to, and use, a wider and more sophisticated range of technology than what is available in the animal tracking sphere. Thus, this may be a critical time to bring together animal biology and medical technology, so that future research can draw inspiration across disciplines.

While biologging has largely focused on describing *where* animals go, the field of 'physiologging' (i.e. animal attached logging of physiological variables such as heart rate, blood oxygen content, lactate, breathing frequency and tidal volume) can provide crucial insights into *how* and *why* animals make the journeys they do. Many of the most important research questions in ecology (e.g. how does the environment drive movement? what sensory information do animals use to navigate? how will wildlife cope with anthropogenic-driven climate change?) critically need these *how* and *why* questions to be answered. However, physiologging technologies have evolved much more slowly than biologging technologies, with cutting edge developments generally coming from individual laboratory groups or research projects. From the 1960s onwards, a revolution in microelectronics, sports wearable technologies, nano-sensor devices and portable medical diagnostics for humans has provided a fertile opportunity for a step change in the study of physiology in free-living animals, which does not seem to have been exploited. For example, in 1962, Leyland C. Clark (the inventor of the oxygen electrode) invented the '*enzyme electrode*', which used electrochemical detection of an immobilized enzyme by a metal electrode to measure the concentrations of various substances [19]. These 'biosensors' are now extremely small, can cost as little as 2 cents a test, and can be mass produced in millions of units via screen-printing [20,21]. In a total biosensor market worth more than $13 billion, approximately 85% of the market is now focused on the measurement of blood glucose for diabetes [22]. Yet, these technologies appear to have been almost entirely untapped by the animal biologging field. We therefore propose that a '*second age of biologging*' has arrived, which will operate on the boundaries between the disciplines of animal biology, medicine, sports and engineering, and will enable researchers to answer important questions in eco-physiology. This theme issue was driven by the recognition that animal biology requires a step change in the available technology to answer big research questions, and that the fields of animal biology and sports medical wearables and technology should now be integrated. The theme issue is divided into three sections.

2. Part 1: the past

In the mid-twentieth century, scientists contrived to monitor movements of marine megafauna under natural conditions. For example, Archie Carr used styrofoam floats and helium-filled balloons to track the movement of green turtles in the open sea [23], Per Scholander deployed capillary tubes on a fin whale to measure their maximum dive depth [24], and Arthur DeVries attached a Tsurumi Seiki depth recorder on female Weddell seals to show that these animals could dive down to at least 350 m [25] (figure 1). Following on from the research by Arthur DeVries, Gerald Kooyman then designed and built a time-depth recorder for deployment on Weddell seals to demonstrate that these animals can dive even deeper, as individuals reached depths beyond 600 m and for longer than 40 min [37]. In fact, this particular study may have been the genesis of the field of measuring physiology in free-living animals [38]. In 2003, the first international symposium on such research was held in Tokyo, and a new term '*Bio-logging*' was proposed by the organizing committee. Biologging has now come to be defined as the 'investigation of phenomena in or around free-living organisms that are beyond the boundary of our visibility or experience' [39]. Since then, a biologging symposium has been held every two to three years in several locations around the world. The field of biologging traditionally focused on technologies that allowed researchers to follow the movements of animals via satellite, which resulted in the successful tracking of a diverse range of terrestrial and marine animals [40,41]. However, the field of physiologging did not keep pace, possibly owing to the invasive and logistically demanding nature of physiological research [42] and the size of traditional logging devices that precluded smaller animals from being studied.

3. Part II: the present state-of-the-art

Owing to the recent and rapid development of physiologging technologies, it is currently possible to monitor fine-scale physiological changes in free-living animals not only with custom-made biologging devices [43], but also with state-of-the-art miniaturized commercial technologies developed for use in humans [44] or for farmed terrestrial and aquatic animals (e.g. dairy cattle [45,46] and fishes [47,48]). For example, the portable and commercially available near infraRed spectroscopy data logging devices introduced in 2006 were originally designed for measuring muscle oximetry in sports athletes [49], but have now also been used to show anticipatory adjustments of blood flow prior to diving in seals [18,50,51]. A wide range of variables can be measured with current physiologging technologies, which includes heart rate [52–56], brain activity [57,58], tissue oxygenation [50,51], respiratory rhythms [59,60] and body temperature [61,62]. When measured simultaneously with other parameters (e.g. time, depth, altitude, etc.), these variables can provide substantial insights into how wild animals undertake their remarkable feats of athleticism.

In addition to investigating the eco-physiology of wild animals, studies of animals in managed care provide rich opportunities for developing physiologging technologies, validating sensors, developing automated analytical approaches, and for comprehensively understanding the physiological responses of farmed animals and their longer-term consequences. For example, the global aquaculture industry is valued at several hundred billion dollars and thus optimizing the health and mass gain of fishes and shellfish is of paramount importance. Consequently, tools to monitor aquatic animal movement and physiology have been developed to maximize yield [47,48]. Likewise, automated analysis of physiological and movement data from dairy cows can help to identify and treat lameness before milk production suffers [45]. Furthermore, measurements of physiological parameters in cetaceans that are housed in aquaria and research facilities provide an opportunity to validate algorithms and/or indices for use on free-living animals [59]. Emerging technologies using implanted biosensors with carbon nanotubes [36] or glue-on 'marine skin' devices [64] have not yet been able to make measurements of biological phenomena, but have paved the way for future research.

4. Part III: the future

At present, with few exceptions, the application of physiologging in wild animal research is generally restricted to a handful of laboratories that have in-house engineers designing custom-made devices for their studies [36,63,64]. By introducing the field of biologging to medical biotechnology and sports wearables, as well as technology used in managed animals (agriculture and aquaculture), the hope is that the field can be opened up to allow more researchers to ask the sorts of questions that are required to tackle the most important threats to wild animals (e.g. disease transmission, climate change, [65]). Moreover, because devices developed for the medical biotechnology, agricultural and sports industries are underlined by enormous market opportunity, they are generally better tested and thus have a lower failure rate (e.g. from leaking or breaking, to hardware and software failures). This means that animal researchers employing these technologies could get more accurate and reliable data over longer periods of time, which would undoubtedly improve wildlife management, threat mitigation and our understanding of species resilience. This would represent a considerable step forward for wild animal research [65,66]. At the same time, automated analytical and software approaches will increase the power of analyses while also transforming potentially complex physiologging technologies into more user-friendly systems [67]. This may also have the advantage of helping to alleviate some of the problems that can be encountered when processing the long-term and/or high-resolution datasets obtained with physiologging technologies (e.g. the sampling of an electrocardiogram signal at 200 Hz for an entire year would produce 6.3 billion data points) [68]. The development of small and robust devices for measuring the physiology of wild animals also represents an exciting engineering challenge that could be used in the microelectronics realm to drive device development and testing in a broader sense. Finally, lessons learned from how animals cope with extreme environments and undertake (at least what we perceive to be) extreme athletic feats may yield lessons for the treatment of human conditions [69,70]. For example, the study of hypoxia in high-flying birds has been of interest to medics studying ischemia and hypoxaemia in humans [71].

5. Concluding remarks

The study of free-living animals and wildlife continues to provide a rich ground for scientific discovery and technical development (e.g. the ICARUS global tracking initiative [72]). Excitingly, biologging and its sub-discipline physiologging are poised to greatly benefit from the rapid advancements in medical biotechnology and wearable biosensors. With an ever-increasing access to technologies capable of determining real-time physiological changes in free-living animals, a '*second age of biologging*' has well and truly arrived for eco-physiologists. This age will undoubtedly create new and exciting opportunities for measuring biological phenomena in free-living animals. Such information will not only provide important information about basic function and physiology, but will be critical to predict how major forces such as disease and climate change may impact the performance, health and welfare of both individuals and populations of free-living animals.

Data accessibility. This article has no additional data.

Competing interests. We declare we have no competing interests.

Funding. We received no funding for this study.

Acknowledgements. This manuscript benefitted enormously from the careful, thorough and constructive comments of Jeroen Brijs and two anonymous reviewers. This special issue is dedicated to Professor Patrick Butler, who was one of the pioneers in the study of the physiology of free-living animals, and thus inspired the field on which physiologging has been developed.

References

1. Gill RE *et al.* 2009 Extreme endurance flights by landbirds crossing the Pacific Ocean: ecological corridor rather than barrier? *Proc. R. Soc. B* **276**, 447–457. (doi:10.1098/rspb.2008.1142)
2. Egevang C, Stenhouse IJ, Phillips RA, Petersen A, Fox JW, Silk JRD. 2010 Tracking of Arctic terns *Sterna paradisaea* reveals longest animal migration. *Proc. Natl Acad. Sci. USA* **107**, 2078–2081. (doi:10.1073/pnas.0909493107)
3. Bishop CM *et al.* 2015 The roller coaster flight strategy of bar-headed geese conserves energy during Himalayan migrations. *Science* **347**, 250–254. (doi:10.1126/science.1258732)
4. Hawkes LA *et al.* 2012 The paradox of extreme high-altitude migration in bar-headed geese *Anser indicus*. *Proc. R. Soc. B* **280**, 20122114. (doi:10.1098/rspb.2012.2114)
5. Hawkes LA *et al.* 2011 The trans-Himalayan flights of bar-headed geese (*Anser indicus*). *Proc. Natl Acad. Sci. USA* **108**, 9516–9519. (doi:10.1073/pnas.1017295108)
6. Klaassen RHG, Alerstam T, Carlsson P, Fox JW, Lindström Å. 2011 Great flights by great snipes: long and fast non-stop migration over benign habitats. *Biol. Lett.* **7**, 833. (doi:10.1098/rsbl.2011.0343)
7. Hedenström A, Norevik G, Warfvinge K, Andersson A, Bäckman J, Åkesson S. 2016 Annual 10-month aerial life phase in the common swift *Apus apus*. *Curr. Biol.* **26**, 3066–3070. (doi:10.1016/j.cub.2016.09.014)
8. Wienecke B, Robertson G. 2006 Comparison of foraging strategies of incubating king penguins *Aptenodytes patagonicus* from Macquarie and Heard islands. *Polar Biol.* **29**, 424–438. (doi:10.1007/s00300-005-0074-5)
9. Meir JU, Champagne CD, Costa DP, Williams CL, Ponganis PJ. 2009 Extreme hypoxemic tolerance and blood oxygen depletion in diving elephant seals. *Am. J. Physiol. Reg. Integr. Comp. Physiol.* **297**, R927–RR39. (doi:10.1152/ajpregu.00247.2009)
10. Hindell MA, Slip DJ, Burton HR, Bryden MM. 1992 Physiological implications of continuous, prolonged, and deep dives of the southern elephant seal (*Mirounga leonina*). *Can. J. Zool.* **70**, 370–379. (doi:10.1139/z92-055)
11. McIntyre T, de Bruyn PJN, Ansorge IJ, Bester MN, Bornemann H, Plotz J, Tosh CA. 2010 A lifetime at depth: vertical distribution of southern elephant seals in the water column. *Polar Biol.* **33**, 1037–1048. (doi:10.1007/s00300-010-0782-3)
12. Schorr GS, Falcone EA, Moretti DJ, Andrews RD. 2014 First long-term behavioral records from Cuvier's beaked whales (*Ziphius cavirostris*) reveal record-breaking dives. *PLoS ONE* **9**, e92633. (doi:10.1371/journal.pone.0092633)
13. Quick NJ, Cioffi WR, Shearer JM, Fahlman A, Read AJ. 2020 Extreme diving in mammals: first estimates of behavioural aerobic dive limits in Cuvier's beaked whales. *J. Exp. Biol.* **223**, jeb222109. (doi:10.1242/jeb.222109)
14. Simaika JP, Samways MJ. 2010 Biophilia as a universal ethic for conserving biodiversity. *Conserv. Biol.* **24**, 903–906. (doi:10.1111/j.1523-1739.2010.01485.x)
15. Berger MM, Grocott MPW. 2017 Facing acute hypoxia: from the mountains to critical care medicine. *Br. J. Anaesth.* **118**, 283–286. (doi:10.1093/bja/aew407)
16. Grocott MPW, Martin DS, Levett DZH, McMorrow R, Windsor J, Montgomery HE. 2009 Arterial blood gases and oxygen content in climbers on Mount Everest. *New Engl. J. Med.* **360**, 140–149. (doi:10.1056/NEJMoa0801581)
17. Ponganis PJ, Stockard TK, Meir JU, Williams CL, Ponganis KV, van Dam RP, Howard R. 2007 Returning on empty: extreme blood O_2 depletion underlies dive capacity of emperor penguins. *J. Exp. Biol.* **210**, 4279–4285. (doi:10.1242/jeb.011221)
18. Mcknight JC *et al.* 2019 Shining new light on mammalian diving physiology using wearable near-infrared spectroscopy. *PLoS Biol.* **17**, e3000306. (doi:10.1371/journal.pbio.3000306)
19. Updike SJ, Hicks GP. 1967 The enzyme electrode. *Nature* **214**, 986–988. (doi:10.1038/214986a0)
20. Turner APF. 2013 Biosensors: sense and sensibility. *Chem. Soc. Rev.* **42**, 3184. (doi:10.1039/c3cs35528d)
21. Yetisen AK, Akram MS, Lowe CR. 2013 Paper-based microfluidic point-of-care diagnostic devices. *Lab. Chip* **13**, 2210–2251. (doi:10.1039/c3lc50169h)
22. Metkar SK, Girigoswami K. 2019 Diagnostic biosensors in medicine – a review. *Biocatal. Agricult. Biotechnol.* **17**, 271–283. (doi:10.1016/j.bcab.2018.11.029)
23. Carr A. 1965 The navigation of the green turtle. *Sci. Am.* **212**, 78–87. (doi:10.1038/scientificamerican0565-78)
24. Scholander PF. 1940 Experimental investigations on the respiratory function in diving mammals and birds. *Hvalradets Skrifter* **22**, 1–131.
25. DeVries AL, Wohlschlag DE. 1964 Diving depths of the Weddell seal. *Science* **145**, 292. (doi:10.1126/science.145.3629.292)
26. Eliassen E. 1962 Preliminary results from new methods of investigating the physiology of birds during flight. *Ibis* **105**, 234–237. (doi:10.1111/j.1474-919X.1963.tb02497.x)
27. Frank TH. 1968 Telemetering the electrocardiogram of free swimming *Salmo Irideus*. *IEEE Trans. Biomed. Eng.* **2**, 111–114. (doi:10.1109/TBME.1968.4502546)
28. Kooyman GL. 1966 Maximum diving capacities of the Weddell seal (*Leptonychotes weddelli*). *Science* **151**, 1553–1554. (doi:10.1126/science.151.3717.1553)
29. Woakes AJ, Butler PJ. 1975 An implantable transmitter for monitoring heart rate and respiratory frequency in diving ducks. *Biotelemetry* **2**, 153–160.
30. Priede IG. 1984 A basking shark (*Cetorhinus maximus*) tracked by satellite together with simultaneous remote sensing. *Fish. Res.* **2**, 201–216. (doi:10.1016/0165-7836(84)90003-1)
31. Hill RD, Schneider RC, Schuette AH, Zapol WM. 1983 Microprocessor-controlled monitoring of bradycardia in free-diving Weddell seals. *Antarct. J. US* **28**, 213–214.
32. Hill RD. 1986 Microcomputer monitor and blood sampler for free- diving Weddell seals. *J. Appl. Physiol.* **61**, 1570–1576. (doi:10.1152/jappl.1986.61.4.1570)
33. Wilson RP, Cooper J, Plotz J. 1992 Can we determine when marine endotherms feed? A case study with seabirds. *J. Exp. Biol.* **167**, 267–275. (doi:10.1242/jeb.167.1.267)
34. Vyssotski AL, Serkov AN, Itskov PM, Dell'Omo G, Latanov AV, Wolfer DP, Lipp HP. 2006 Miniature neurologgers for flying pigeons: multichannel EEG and action and field potentials in combination with GPS recording. *J. Neurophysiol.* **95**, 1263–1273. (doi:10.1152/jn.00879.2005)
35. Wilmers CC, Nickel B, Bryce CM, Smith JA, Wheat RE, Yovovich V. 2015 The golden age of bio-logging: how animal-borne sensors are advancing the frontiers of ecology. *Ecology* **96**, 1741–1753. (doi:10.1890/14-1401.1)
36. Lee MA *et al.* 2019 Implanted nanosensors in marine organisms for physiological biologging: design, feasibility, and species variability. *ACS Sens.* **4**, 32–43. (doi:10.1021/acssensors.8b00538)
37. Kooyman GL. 1965 Techniques used in measuring diving capacities of Weddell seals. *Polar Rec.* **12**, 391–394. (doi:10.1017/S003224740005484X)
38. Williams CL, Ponganis PJ. 2021 Diving physiology of marine mammals and birds: the development of biologging techniques. *Phil. Trans. R. Soc. B* **376**, 20200211. (doi:10.1098/rstb.2020.0211)
39. Boyd IL, Kato A, Ropert-Coudert Y. 2004 Bio-logging science: sensing beyond the boundaries. *Mem. Natl Inst. Polar Res. Spec. Issue* **58**, 1–14.
40. Hussey NE *et al.* 2015 Aquatic animal telemetry: a panoramic window into the underwater world. *Science* **348**, 1255642. (doi:10.1126/science.1255642)

41. Kays R, Crofoot MC, Jetz W, Wikelski M. 2015 Terrestrial animal tracking as an eye on life and planet. *Science* **348**, aaa2478. (doi:10.1126/science.aaa2478)
42. Palmer A, Greenhough B. 2021 Out of the lab, into the field: perspectives on social, ethical, and regulatory challenges in UK wildlife research. *Phil. Trans. R. Soc. B* **376**, 20200226. (doi:10.1098/rstb.2020.0226)
43. Laske TG, Garshelis DL, Iles TL, Iaizzo PA. 2021 An engineering perspective on the development and evolution of implantable cardiac monitors in free-living animals. *Phil. Trans. R. Soc. B* **376**, 20200217. (doi:10.1098/rstb.2020.0217)
44. MacDonald A, Hawkes LA, Corrigan DK. 2021 Recent advances in medical sensing and biosensor technologies and their potential application in the study of physiology in wild animals. *Phil. Trans. R. Soc. B* **376**, 20200228. (doi:10.1098/rstb.2020.0228)
45. King A. 2017 Technology: the future of agriculture. *Nature* **544**, S21–SS3. (doi:10.1038/544S21a)
46. Jukan A, Masip-Bruin X, Amla N. 2017 Smart computing and sensing technologies for animal welfare: a systematic review. *ACM Comput. Surv.* **50**, Article 10. (doi:10.1145/3041960)
47. Brijs J, Føre M, Gräns A, Clark TD, Axelsson M, Johansen JL. 2021 Bio-sensing technologies in aquaculture: how remote monitoring can bring us closer to our farm animals. *Phil. Trans. R. Soc. B* **376**, 20200218. (doi:10.1098/rstb.2020.0218)
48. Su X, Sutarlie L, Jun Loh X. 2020 Sensors, biosensors, and analytical technologies for aquaculture water quality. *Research* **2020**, 8272705.
49. Perrey S, Ferrari M. 2018 Muscle oximetry in sports science: a systematic review. *Sports Med.* **48**, 597–616. (doi:10.1007/s40279-017-0820-1)
50. Mcknight JC *et al.* 2021 When the human brain goes diving: using NIRS to measure cerebral and systemic cardiovascular responses to deep. Breath-hold diving in elite freedivers. *Phil. Trans. R. Soc. B* **376**, 20200349. (doi:10.1098/rstb.2020.0349)
51. Mcknight JC *et al.* 2021 Shining new light on sensory brain activation and physiological measurement in seals using wearable optical technology. *Phil. Trans. R. Soc. B* **376**, 20200224. (doi:10.1098/rstb.2020.0224)
52. Linek N, Volkmer T, Shipley JR, Twining CW, Zúñiga D, Wikelski M, Partecke J. 2021 A songbird adjusts its heart rate and body temperature in response to season and fluctuating daily conditions. *Phil. Trans. R. Soc. B* **376**, 20200213. (doi:10.1098/rstb.2020.0213)
53. Twardek WM, Ekström A, Eliason EJ, Lennox RJ, Tuononen E, Abrams AEI, Jeanson AL, Cooke SJ. 2021 Field assessments of heart rate dynamics during spawning migration of wild and hatchery-reared Chinook salmon. *Phil. Trans. R. Soc. B* **376**, 20200214. (doi:10.1098/rstb.2020.0214)
54. Aoki K, Watanabe YY, Inamori D, Funasaka N, Sakamoto KQ. 2021 Towards non-invasive heart rate monitoring in free-ranging cetaceans: a unipolar suction cup tag measured the heart rate of trained Risso's dolphins. *Phil. Trans. R. Soc. B* **376**, 20200225. (doi:10.1098/rstb.2020.0225)
55. Sakamoto KQ, Miyayama M, Kinoshita C, Fukuoka T, Ishihara T, Sato K. 2021 A non-invasive system to measure heart rate in hard-shelled sea turtles: potential for field applications. *Phil. Trans. R. Soc. B* **376**, 20200222. (doi:10.1098/rstb.2020.0222)
56. Wascher CAF. 2021 Heart rate as a measure of emotional arousal in evolutionary biology. *Phil. Trans. R. Soc. B* **376**, 20200479. (doi:10.1098/rstb.2020.0479)
57. Aulsebrook AE, Connelly F, Johnsson RD, Jones TM, Mulder RA, Hall ML, Vyssotski AL, Lesku JA. 2020 White and amber light at night disrupt sleep physiology in birds. *Curr. Biol.* **30**, 3657–3663. (doi:10.1016/j.cub.2020.06.085)
58. Lyamin OI, Kosenko PO, Korneva SM, Vyssotski AL, Mukhametov LM, Siegel JM. 2018 Fur seals suppress REM sleep for very long periods without subsequent rebound. *Curr. Biol.* **28**, 2000–2005. (doi:10.1016/j.cub.2018.05.022)
59. Blawas AM, Nowacek DP, Rocho-Levine J, Robeck TR, Fahlman A. 2021 Scaling of heart rate with breathing frequency and body mass in cetaceans. *Phil. Trans. R. Soc. B* **376**, 20200223. (doi:10.1098/rstb.2020.0223)
60. Hooker SK, Andrews RD, Arnould JPY, Bester MN, Davis RW, Insley SJ, Gales NJ, Goldsworthy SD, McKnight JC. 2021 Fur seals do, but sea lions don't—cross taxa insights into exhalation during ascent from dives. *Phil. Trans. R. Soc. B* **376**, 20200219. (doi:10.1098/rstb.2020.0219)
61. Parr N, Bishop CM, Batbayar N, Butler PJ, Chua B, Milsom WK, Scott GR, Hawkes LA. 2019 Tackling the Tibetan Plateau in a down suit: insights into thermoregulation by bar-headed geese during migration. *J. Exp. Biol.* **222**, jeb203695. (doi:10.1242/jeb.203695)
62. Trondrud LM *et al.* 2021 Determinants of heart rate in Svalbard reindeer reveal mechanisms of seasonal energy management. *Phil. Trans. R. Soc. B* **376**, 20200215. (doi:10.1098/rstb.2020.0215)
63. Nassar JM, Khan SM, Velling S. 2018 Compliant lightweight non-invasive standalone 'Marine Skin' tagging system. *Flex. Electron.* **2**, 13. (doi:10.1038/s41528-018-0025-1)
64. Kaidaorva A, Marengo M, Marinaro G, Geraldi NR, Wilson R, Duarte CM, Kosel J. 2019 Flexible, four-electrode conductivity cell for biologging applications. *Results Mat.* **1**, 100009. (doi:10.1016/j.rinma.2019.100009)
65. Williams HJ, Shipley JR, Rutz C, Wikelski M, Wilkes M LAH. 2021 Future trends in measuring physiology in free-living animals. *Phil. Trans. R. Soc. B* **376**, 20200230. (doi:10.1098/rstb.2020.0230)
66. Cooke SJ *et al.* 2021 One hundred research questions in conservation physiology for generating actionable evidence to inform conservation policy and practice. *Conserv. Physiol.* **9**, coab009. (doi:10.1093/conphys/coab009)
67. Wilson RP, Holton MD, Teilmann J, Siebert U. 2021 Animal tag technology keeps coming of age: an engineering perspective. *Phil. Trans. R. Soc. B* **376**, 20200229. (doi:10.1098/rstb.2020.0229)
68. Harrison X. 2021 A brief introduction to the analysis of time series data from biologging studies. *Phil. Trans. R. Soc. B* **376**, 20200227. (doi:10.1098/rstb.2020.0227)
69. Ponganis PJ. 2019 State of the art review: from the seaside to the bedside: insights from comparative diving physiology into respiratory, sleep and critical care. *Thorax* **74**, 512–518. (doi:10.1136/thoraxjnl-2018-212136)
70. Williams TM, Davis RW. 2021 Physiological resiliency in diving mammals: insights on hypoxia protection using the Krogh principle to understand COVID-19 symptoms. *Comp. Biochem. Physiol. Part A Mol. Integr. Physiol.* **253**, 110849. (doi:10.1016/j.cbpa.2020.110849)
71. Wilkes M, MacInnis MJ, Witt MJ, Vergalla M, Thomas A, Hawkes LA. 2017 Free flight physiology: paragliding and the study of extreme altitude. *High Alt. Med. Biol.* **18**, 90–91. (doi:10.1089/ham.2016.0135)
72. Belyaev MY, Volkov ON, Solomina ON, Weppler J, Mueller U, Tertitski GM, Wikelski M, Pitz W. 2020 Development of technology for monitoring animal migration on Earth using scientific equipment on the ISS RS. In *IEEE Trans. Biomed. Eng. 27th Saint Petersburg Int. Conf. on Integrated Navigation Systems (ICINS)*, pp. 1–7. (doi:10.23919/ICINS43215.2020.9133883)