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Advances in bio-logging techniques and their application to study navigation in wild seabirds

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ABSTRACT

This review summarizes the advances in bio-logging technology that enables us to monitor foraging behavior, movement, behavioral performance, physiological performance, and sociality in a wide range of bird species, as well as their habitat. Subsequently, navigation is discussed, using long-distance movements in streaked shearwaters as a case study. Moreover, challenges and future research directions in bio-logging science are presented, with focus on: multimodal recording, big data analysis, feedback logging, low-power consumption and power generation systems, logger effects, and capture–recapture methods.

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1. Introduction

Animal behavior has evolved under complex natural environments; therefore, behavior should be observed in natural environments, to understand its functions, mechanisms, and development. Focal animal sampling (i.e. observation of a target individual), and the continuous recording of behavior *in situ*, for centuries, have been the standard and essential approaches in the study of ethology, ecology, and evolution [1]. ‘Bio-logging,’ i.e. the use of animal-borne sensors, is a contemporary focal sampling method that enables us to integrate the study of movements, behavior, physiology, and the environments of animals, at various spatial and temporal scales that are inaccessible to humans [2–13]. Since the first depth recorders were attached to the Weddell seals [14], over the last three decades there have been extraordinary improvements in sensors, batteries, and memories of animal-borne devices. The derived data is particularly useful in studying varied behavioral aspects of animals, viz., habitat selection, migration, dispersion, and foraging strategies [15]. Recently, bio-logging has inspired a variety of research fields, including robotics [16] and human mobility research [17]. One of the most ambitious bio-logging projects – ‘Systems Science of Bio-Navigation’ – has been initiated as a Grant-in-Aid for Scientific Research on Innovative Areas (JSPS, Japan) and aims to obtain an unprecedented amount of behavioral data by

deploying bio-logging devices including a cutting-edge logger called ‘Log-bot’ (Logging Robot).

Bio-logging provides two perspectives: one is the first-person perspective, in which a researcher sees the world through the eyes of the animal (e.g. using video loggers); the other is the third-person perspective, in which a researcher sees animal behavior and physiology from a higher, objective perspective (e.g. using GPS loggers). Although time-series data are obtained from both perspectives, different analytical methods can be applied on the data. For example, image-processing techniques for wearable cameras may be used in the former approach [18], while time–frequency analyses are often used in the latter [19]. It is also necessary to develop integrative methods to link data generated by studies conducted from different perspectives.

In bio-logging, data are stored in loggers and downloaded later when the loggers are recovered, whereas in ‘bio-telemetry,’ data is sent to receivers or satellites. However, some devices have a latency in data transmission – storing data for a while and then transmitting it to signal receivers or satellites; therefore, the differences between bio-logging and bio-telemetry are often ambiguous. In this article, the use of animal-mounted sensors is referred to as ‘bio-logging,’ irrespective of the ways in which data are logged and transmitted. I focus mainly on bird species, because birds are well studied

by bio-logging. The studies I review have tackled the challenges of miniaturization of the devices, and the development of sophisticated sensors for birds.

2. Advanced bio-logging and its applications

2.1. Foraging

Foraging (i.e. searching for food and eating it) is one of the most important animal behavioral components. Several measures have been used as proxies of feeding in birds. Ingestion of prey items and breathing can be monitored using a Hall sensor attached to one mandible and a magnet attached to the other [20]. A temperature logger placed in the stomach or esophagus provides information on the reduction in temperature when endotherms feed on cold prey items, allowing prey size to be estimated [21]. Digestion can be monitored using gastric pH loggers [22].

The use of video-camera loggers is now extremely widespread, particularly in documenting the searching and ingesting behavior of predators [23–25]. Video loggers can also be used to understand how animals utilize visual cues for pursuing individual prey [26], and use tools for foraging [27]. However, video loggers consume considerable battery power for recording movies, which are several hours long for birds with a body mass of 500 g (e.g. streaked shearwater, see below). The recording capacity of most video loggers cannot cover a round trip for foraging (i.e. a basic unit of behavior during breeding season) ranging from several hours to days. Accordingly, future solutions to circumvent battery limitations are needed.

2.2. Movement

Animal tracking technology enables us to track the movement of animals at various spatial and temporal scales. GPS loggers can be used to calculate the locations and movement of animals [28–30] (Figure 1), and the movement of the tagged animals can be tracked using radio-telemetry or satellite transmitters without recapturing the animal [31]. Given that satellite-linked tag failure (e.g. owing to battery depletion) can be reliably distinguished from probable target animal deaths, through careful inspection of the data, the mortality status of birds can be inferred [31–33].

Dead-reckoning technologies reconstruct 3D trajectories using speed and heading [34,35]. Altimeters also help explain flight adaptations that enable the exploitation of 3D space and extraordinary environments [36], for example, geese flying over the Himalayan mountains [37].

Radio frequency identification (RFID) tags allow the presence of tagged animals to be monitored at fixed RFID reading stations; by connecting the information on the presence of animals, movements can be studied [38].

Light-intensity loggers calculate local sunrise, sunset, and length of day, enabling researchers to estimate latitudinal and longitudinal coordinates [39]. Miniaturized light-intensity loggers are now sufficiently light-weight (less than 1 g) to be attached to small birds. For example, this technology has been utilized to show that passerine birds with a body mass of 50 g, and terns of 100 g, migrate from North America to the Amazon [40], and from Greenland to the shores of Antarctica [41], respectively.

2.3. Behavioral performance

Accelerometers and gyroscopes have been instrumental in quantifying animal motions in biomechanics studies [42,43]. For example, data generated by accelerometers have revealed that diving seabirds use both the upstroke and the downstroke against buoyancy at shallow depths, while they rely mainly on the downstroke as they descend deeper, to increase locomotor efficiency [44].

Accelerometers are also used for calculating behavioral time budgets and for analyzing behavioral development [45–47]. Using an accelerometer, it was shown that swifts are airborne for most of the time during their non-breeding period [48]. Data generated by accelerometers, video, and GPS loggers have shown that juvenile boobies have low-flight maneuverability [49], but they gradually acquire efficient flight [50,51] and diving skills [52] during the post-fledging period, which might be the proximate cause of prolonged post-fledging care in this species.

2.4. Physiological performance

Physiological loggers that monitor body temperature [53], heart rates [54,55], blood partial pressure of oxygen [56], and glucose levels in blood [57] can be used to record physiological states, physiological adaptation, and stress responses in animals [58]. For example, data from heart-rate loggers attached to seabirds showed that heart rate during flight does not differ from that during resting at the sea surface, indicating a physiological adaptation to long-distance flight over the ocean [59]. Some physiological parameters are still difficult to measure, necessitating further innovations in this field. For example, the blood glucose levels of fish can be estimated by measuring the glucose levels in the interstitial fluid behind the eyeball, which correlates with blood glucose levels; it is also comparatively easy to deploy a glucose biosensor on free-moving animals [57].

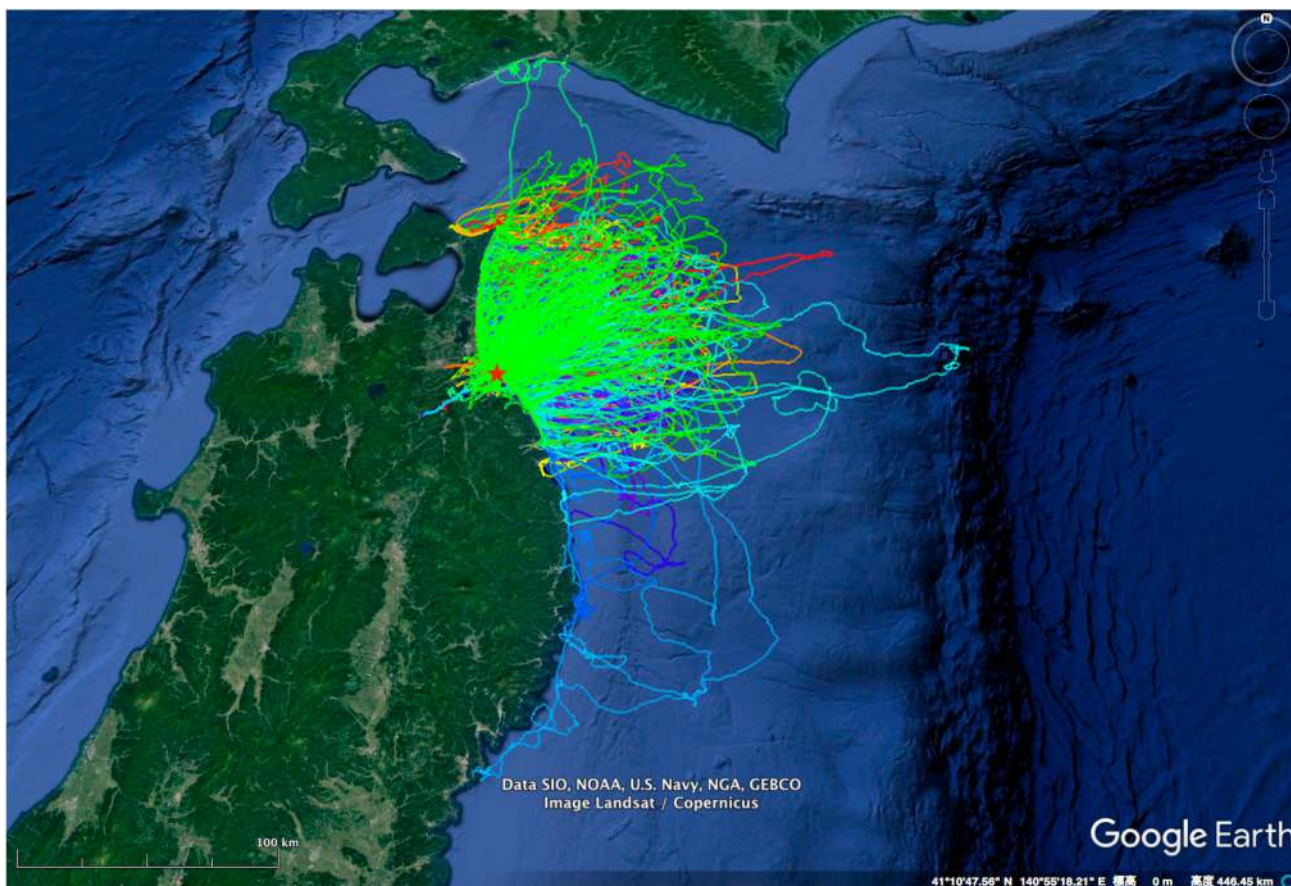


Figure 1. GPS trajectories obtained from black-tailed gulls (*Larus crassirostris*). The star indicates the position of the breeding island.

Electroencephalogram (EEG) recordings reveal changes in the neurological states in response to environmental signals. When pigeons cross visual landmarks such as highways, particular changes in EEG are observed [60]. EEG loggers also reveal that frigatebirds sleep during flight over the ocean [61].

Accelerometers have revolutionized animal energy-expenditure estimation, with the sum of the absolute values of dynamic acceleration correlating with energy expenditure [62,63].

Physiological parameters of animals can be calculated from bio-logging data and mechanical models. Air volume in the lungs and air sacs of diving penguins has been estimated from swimming speed, depth, and acceleration data, using the biomechanical model of ascension during the last phase of the dive [42].

2.5. Environment

Bio-logging data now plays a significant role in environmental data collection, especially of oceanographic data [64]. Animal-borne instruments have been used to sample *in situ* oceanographic data, such as ambient temperature, oxygen concentration, salinity, and

sound [65–67]. Studies on deep-diving animals use conductivity-temperature-depth data loggers to identify temperature signatures, thereby revealing large-scale ocean fronts [68,69]. Animal-mounted cameras can reveal the unknown ecology (e.g. distribution) of prey species such as jellyfish and squid [70,71]. An innovative example is where albatrosses, wearing radar loggers that record radio emissions from fishing vessels, become patrollers of the ocean, allowing fishing vessels to be monitored, including those fishing illegally [72].

Individual animal behavior contains environmental information, because animal behavior is affected by the surrounding environment [73]; therefore, bio-logging data can be used to reconstruct environmental fluctuations in time and space. Soaring seabirds that fly tortuously reveal ground speed fluctuation due to tailwinds and headwinds, enabling the estimation of wind speed and direction experienced by the birds [74]. When seabirds rest on water surface, they tend to be passive drifters, thus providing a direct and detailed description of ocean surface currents [75]. By assimilating high-resolution seabird drift data into an operational ocean forecast system, the accuracy of ocean current forecasts is improved [76].

An index of prey-patch quality (i.e. food abundance or availability for animals) can be estimated by assuming that diving animals maximize energy-gain efficiency, and that resting phases on the water surface are a physiological reaction to the dive duration [77]. In other words, an ‘inverse problem approach’ can be used to indirectly evaluate external factors – prey-patch quality in this case – from animal behavior, because marine animals are expected to adjust their foraging behavior in relation to prey-patch quality. Prey-patch quality for marine predators can be directly monitored by active acoustic loggers [78].

Highly mobile seabirds, with broad foraging ranges, can become effective monitors of regional marine pollution, when the amount of persistent organic pollutants in the oil of the preen glands of the GPS-tagged birds is used as an indicator, for example [79].

2.6. Sociality

Individual animals aggregate socially and make collective decisions to coordinate their actions. Although bio-logging in itself measures behavior at an individual level, some bio-logging approaches enable us to measure local interactions among group members, and infer collective decision-making of animals in the field. For example, data from video loggers showed that young seabirds voluntarily followed other birds, which may directly enhance their foraging success and improve foraging and flying skills during their developmental stage [25]. Data from GPS loggers attached to pigeons suggested that homing pigeons flying in flocks show a leadership hierarchy among members [80]. Data from sound loggers showed that seabirds use acoustic communication when foraging at sea to avoid collisions between individuals [81].

Recently developed proximity- or transceiver loggers can actively record animal sociality. They record the proximity and duration of bird encounters, revealing any close-range associations between non-family birds [82].

3. Case study: the navigation of seabirds

Animals navigate using various cues, which may be visual, magnetic, olfactory, or chemical. Navigation (i.e. movement to a goal) has been well studied in the fields of animal behavior, cognitive science, neuroscience, endocrinology, and morphology. However, until recently, it has been difficult to record animal movements at different spatiotemporal scales, and research has often been limited to small-scale indoor experiments. Advances in bio-logging now make it more viable to explore navigation in the field.

Here, I introduce bio-logging approaches to the analysis of long-distance navigation in animals moving over oceans, using streaked shearwaters (*Calonectris leucomelas*, Figure 2) as a case study. During the chick-rearing period, shearwaters feed on small pelagic fish in offshore areas, up to 1000 km from their breeding colonies, and bring back fish to their chicks [83,84]. Appropriate growth of chicks implies that adults are able to navigate over the ocean successfully, but information on how adults navigate is limited.

Heading vectors of birds and wind vectors were simultaneously modeled and estimated from positional data recorded using animal-borne GPS loggers [85]. The estimated parameters showed that homing shearwaters could head in a direction different from that leading directly to the colony, to offset wind effects, whilst their overall movement took them in the direction of the colony. Streaked shearwaters adopt a dynamic soaring flight, in which their heading direction changes continuously within the scale of a few seconds. Thus, the shearwaters evaluate the wind conditions they experience, and control their flight direction during dynamic soaring, resulting in an optimal navigation course toward their goal on a large spatial scale.

Likewise, we can infer animals’ decision rules by analyzing bio-logging data, and recommend the following procedure: (1) record input and output information, such as that on the environment and/or behavior, (2) estimate parameters such as heading direction by constructing physical or cognitive models that describe the local properties of animals, and (3) establish the decision-making process during long-distance navigation by using correlation, or applying the obtained parameters to movement simulations [85].

It is crucial to adjust time appropriately in spatiotemporally heterogeneous environments for successful long-distance navigation. In the case of the streaked shearwaters, arrivals at the colony from foraging areas are concentrated within a few hours after sunset, independent of the distances between the colony and the foraging areas. How are these birds able to be so punctual? GPS data showed that the initiation time of homing was brought forward in accordance with the expected increase in travel time, based on their homeward distance and average movement speed [86]. These results highlight the high cognitive ability of seabirds regarding space and time.

How animals acquire such navigational ability is one of the most intriguing and important questions in navigation. When the breeding season is over, the adult streaked shearwaters migrate to the seas off New Guinea, northern Australia or the Philippines from November to March for wintering [87]. The birds that migrate from

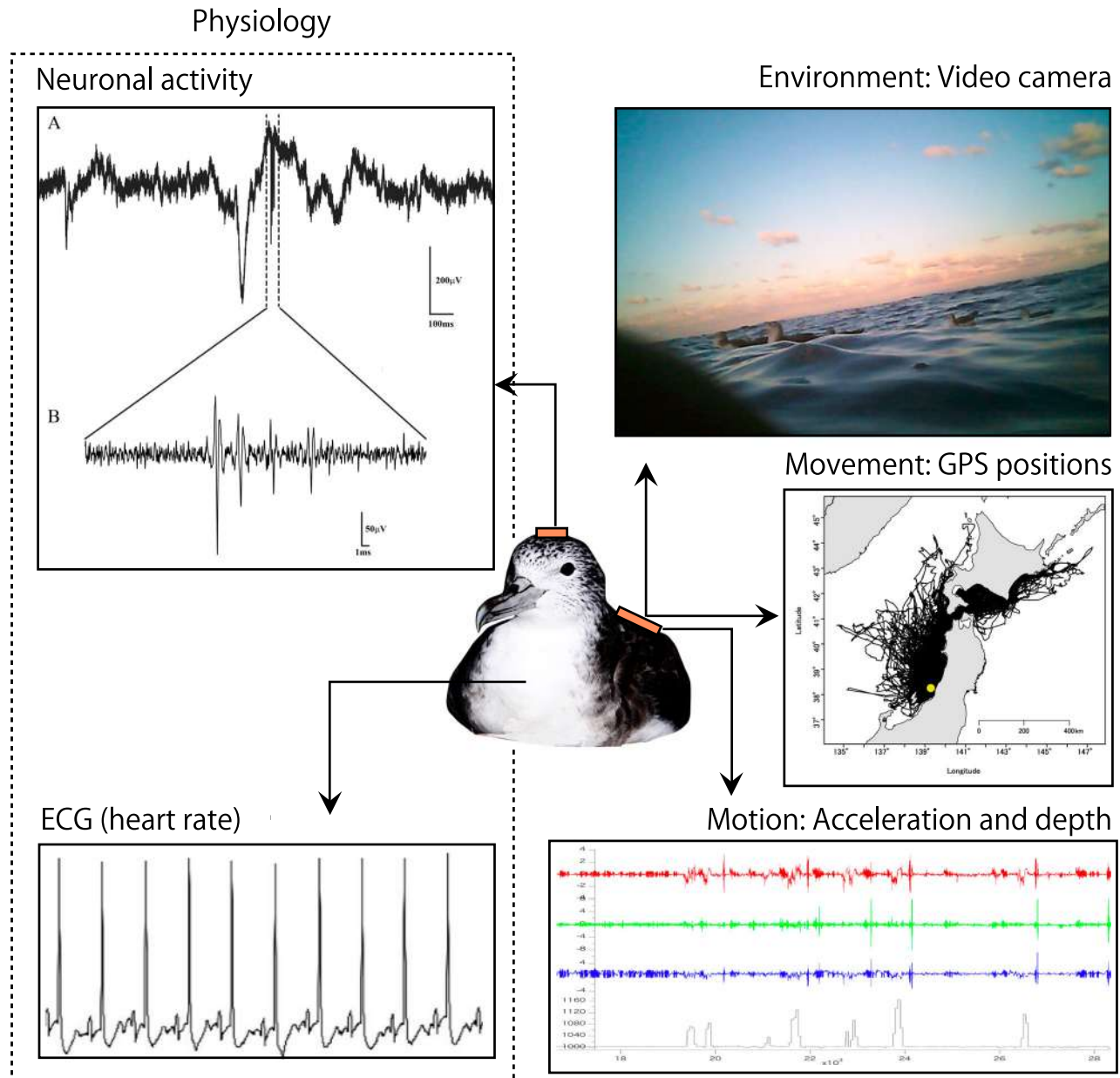


Figure 2. Bio-logging allows biologists to study behavior (e.g. movement, motion), physiology (e.g. neuronal activity, heart rate), and the environment of wild animals, that would be beyond humans' ability to observe. This figure shows examples of bio-logging data obtained from streaked shearwaters. Some parameters can be obtained by multiple channels in a logger (e.g. acceleration and depth sensors), while others can be obtained by simultaneous deployment of several types of loggers (e.g. ECG and video loggers). Unraveling the complex life of an animal species requires the integrated and simultaneous measurements of behavior, physiology, and environment, rather than the assessment of isolated applications of different sensors. (Top left) Neuronal activity recorded from the telencephalon of freely walking shearwater on the ground. A. local field potential (wide-band (1–7 kHz) signal), B. spiking activity (0.8–7 kHz). (Bottom left) ECG (electrocardiogram) wave of an adult shearwater recorded by external ECG logger (after [55]). (Top right) An image obtained from a miniaturized video camera on the back of a shearwater, as it rested on the water surface with other shearwaters. (Middle right) GPS positions of streaked shearwaters. The study colony is indicated by a circle. (Bottom right) Example of a shearwater's dives (black line) and the three-axis acceleration used to quantify diving and flight behavior.

a colony on the north of the large topographic barrier of Honshu Island, Japan, make substantial detours to avoid any landmasses, because shearwaters use dynamic soaring to extract energy for highly efficient travel over oceans. In fact, migrating adults followed one of two

paths that detoured around landmasses that hindered direct southerly migration [31].

Such detours might require experience and skill that inexperienced individuals (first-time migrating fledglings) lack. We deployed GPS-satellite transmitters

on chicks that were close to fledging, to examine how fledglings overcome the challenges of landscape obstacles during migration. In contrast to adults, fledglings performed ‘extreme’ migration, unusual for seabirds, in which they crossed the large landmass of Honshu Island, and flew over mountain ranges [31]. So, how do fledglings subsequently acquire the ability to make detours around landmasses? Detour routes must be learned from individual experience. Fledglings might learn these routes by following adults from the wintering areas to the breeding colonies and/or they might use the long pre-reproductive period to explore the geographical area and form a cognitive map (i.e. a geographical map in their brain).

Trajectory analysis indicates that shearwater fledglings probably use a magnetic inclination compass during their southward migration. Although seabirds have long been thought to use magnetic or smell senses [88], this is still controversial. Knowledge about the mechanisms by which animals navigate in natural environments is limited, with most research being undertaken on passerine birds under laboratory conditions [89]. In future, bio-logging using equipment such as neuronal-activity loggers (Figure 2) may be used to test various hypotheses about navigation mechanisms in freely moving animals (e.g. how do animals sense magnetic fields?).

4. Challenges and future trends

We face several challenges in unraveling the complexity in the life of animal species, although bio-logging provides various forms of data from freely moving animals in the field. Here, I discuss five issues that this review makes apparent. Some of the following limitations have been overcome by the application of emerging technologies such as ‘Log-bots’.

Multimodal recording. Behavior is a dimensional and relational phenomenon [90]; therefore, the recording of multiple channels is needed to record details that might help to explain the behavior and physiology of animals. Add-on sensors for loggers might allow researchers the flexibility to add suitable sensors for their specific research purposes. Also, the control of one sensor, based on a rule that is linked to an animal’s behavior via another sensor (i.e. an event-triggering system, such as a video sensor that turns on only when GPS or acceleration sensors indicate animal foraging), is necessary to optimize the usage of limited battery energy [91].

Big-data analysis. The aggregated information on the behavior, physiology, and environments of animals derived from bio-logging technology constitute big data. In particular, we face the challenge of classifying and integrating time-series bio-logging data. For example, many methods to divide time-series behavior of animals

into discrete chunks have long been developed [92,93]. Recently, the use of machine learning, such as supervised and unsupervised learning, has become more common, with potentially broad applicability in ecological, behavioral, and environmental research over the last decade [94–99]. For example, a trajectory gap can be filled by inverse reinforcement learning [100]. However, mechanisms-based models are also growing in importance [85,101], because machine learning techniques might not be appropriate for revealing biological mechanisms.

Feedback loggers. Correlations do not necessarily infer the causation behind a relationship. For example, the presence of aggregations of predators in areas with high densities of prey does not necessarily mean that the prey attracted the predators; it may be that the predators attracted the prey, using chemical attractants. Causal mechanistic relationships between the behavior, physiology, and environments of animals might be tested by feedback experiments, in which freely moving animals are stimulated, for instance, by their hunger state or motion performance. For example, an automatic weight-release system deployed on a seal revealed that the seal adjusted its stroke patterns according to buoyancy changes, before and after the release of the weight [102]. In future, feedback loggers might permit more active real-time stimulation of animals, involving the sensory, nervous, and physical systems.

Low-power consumption and power generation systems. Issues associated with limited battery-life need to be resolved. Lithium-ion batteries are usually used for data loggers, but additional energy generators would help power-consuming sensors such as video cameras. Solar power is considered to be one of the most practical power sources for loggers, owing to its inexhaustibility and easy availability. However, the effectiveness of solar radiation is affected by the weather, the method of device attachment, and behavior of the target animal [103]. Wind and vibration might be potential sources of power for loggers [104]. To extend the lifetime of the battery, wireless power transfer for loggers could be considered for bird species that conduct round trips between foraging grounds and their nests, where the apparatus should be installed.

Logger effects and capture–recapture methods. Deploying data loggers on animals might produce an adverse effect on their behavior, energetics, reproduction, and survival [105,106]. There may also be immediate stress responses to handling and logger deployment. Heart rate data loggers are of considerable value when quantitatively assessing short-term stress effects on animals. For example, a short period of handling in streaked shearwaters is enough to induce a strong autonomic response, requiring up to 2 h to recover to the resting state [55].

The logger effect should be assessed for both ethical reasons and biological relevance, to ensure that the data accurately reflect the natural behavior of animals. Loggers should weigh less than 3–5% of a bird's body mass [107], but this rule of thumb might differ depending on species and sex. Therefore, a comparison of behavior and reproduction between a control group and a group attached with loggers is necessary to determine the side effects of handling and the loggers themselves. However, a quantitative comparison of behavior *in situ* is impossible in principle in inaccessible areas. To account for this, changes in recorded parameters for different logger sizes are extrapolated to provide estimates for unequipped animals [108].

Refinement of capture and recapture methods is also required [109]. Capture of wild birds is often challenging. Trapping techniques such as mist nets have been used, but new techniques and devices that ensure birds are captured with minimum disturbance should be developed. In particular, unlike transmitters, loggers should be recovered for data acquisition, but capturing the same individual twice is often difficult. To this end, a detachable logger system might be used, with a cable that could be cut remotely [110]. Also, mobile telephone networks might be available for some species that live within the network coverage area [111]. Robot technology may contribute to this important task in bio-logging. For example, communication between animal-borne loggers and aerial drones might enable the retrieval of logged data, far away from the researchers [112].

5. Conclusion

Behavior of animals in the field is not always the same as that under laboratory settings [113]. Bio-logging can bring researchers into the field and generate new hypotheses on animal behavior, as well as test lab-derived hypotheses [114].

Bio-logging has advanced at the interface between science and technology, and may appear to be technology-driven research. Although warnings against being too technology-driven are needed to some extent, we cannot learn what we want to know without the tools to record behavior (e.g. bio-logging). It is important to balance hypothesis- and technology-driven views, as well as analyzing bio-logging data against clear hypotheses.

Over recent years, sensors have evolved, and there has been an Internet revolution; now, the topics of big data and the IoT (Internet of Things) are increasingly discussed. In near future, AI-based loggers, coupled with sensor networks, may develop the potential to become a tool called the IoA (Internet of Animals), which could provide information on the behavior, physiology, and

environment of animals in real time. State-of-the-art bio-logging systems would have applications in a number of different fields, such as conservation [115] (e.g. poaching-alert systems [116]), and invasive animal control [117]. In addition, the integration of bio-logging information (e.g. behavior, physiology, and environment of animals) with robotics can provide people with an experience of moving like an animal in virtual reality [118,119], which may change how they see the world and the relationships among human beings, animals, and environments. Thus, bio-logging may become one of the most potent symbols of biology in the twenty-first century.

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