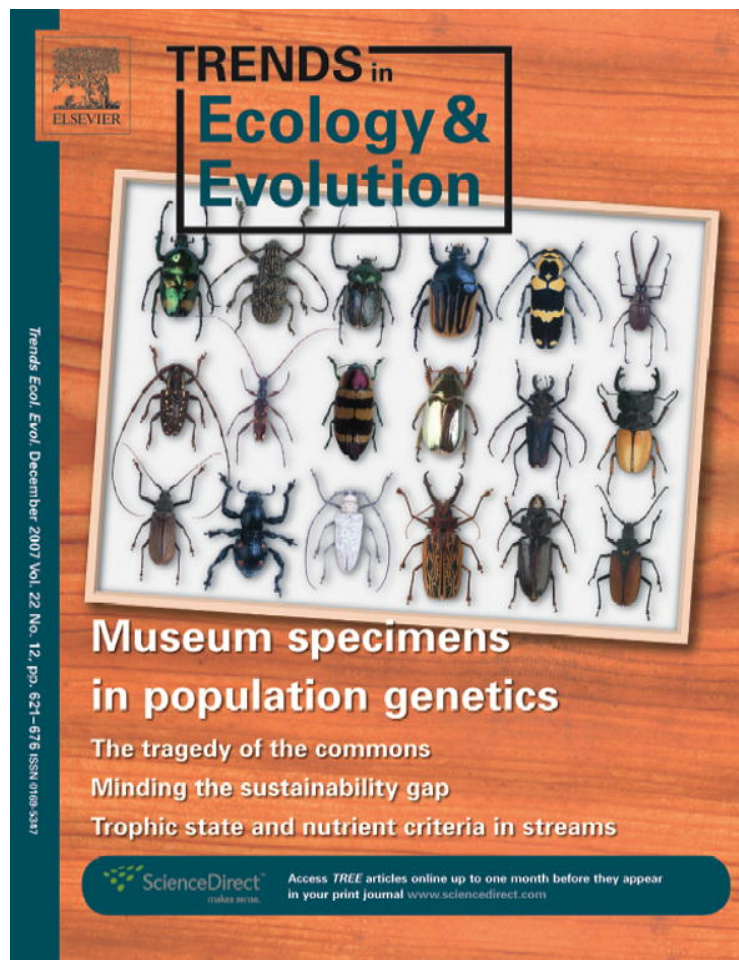


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A new 'view' of ecology and conservation through animal-borne video systems

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Over the past three decades, technological advances for monitoring wild animals have expanded the ability of ecologists to study animal behavior and space use. Currently, researchers are deploying animal-borne video and environmental data collection systems (AVEDs), which enable researchers to see what the animal sees in the field. AVEDs record fine-scale movements as well as features of the surrounding environment and thus provide essential context for understanding animal decisions and interactions with other individuals. These fine-scale data are often crucial for understanding potential conservation threats to species of concern. Here, we discuss the development and research potential offered by AVEDs. The benefits of AVEDs are greatest in hypothesis-driven studies that require a fine-scale perspective that other technologies cannot offer.

Introduction

Animal-borne video and environmental collection systems (AVEDs) [1] are an advanced form of biotelemetry (see Glossary) that enable researchers to see what a wild animal sees in the field and hear what it hears. These systems can also collect physiological and animal location data from other animal-borne sensors (Box 1, Table 1). AVEDs enable continuous video recording of behavior from the perspective of the animal, thereby providing observations of unhabituated, free-ranging species at a finer scale than other techniques can provide (e.g. Refs [2,3]; Figure 1a). Questions about foraging dynamics, reproduction, species interactions (e.g. predator avoidance tactics) and disease transmission often require detailed behavioral data, which AVEDs can provide.

However, AVEDs are rarely viewed as tools of scientific inquiry, perhaps because their public appeal and educational value have been emphasized more than their scientific potential. Unlike many technologies used for ecological research, AVEDs have garnered considerable media exposure. For example, National Geographic's

Crittercam AVEDs headline a weekly television program; the associated website heavily targets children and educators (<http://www.nationalgeographic.com/crittercam>). Given that public policy is as much shaped by public perception as it is by scientific data, this focus is justified [4].

Here, we evaluate the capabilities of AVEDs as instruments for ecological research and discuss the key issues and questions addressed through AVED studies. Despite the availability of other technologies (e.g. still imaging, Box 2, Table 2), we focus on AVEDs because of their rapid development, research potential (i.e. collection of continuous video versus individual snapshots), integration with other sensors, increased application and prevalence in the media. We outline how researchers can maximize the scientific potential of this technology by describing how AVEDs can be used for fine-scale hypothesis testing and bioenergetics research and by

Glossary

Accelerometer: measures acceleration (i.e. changes in motion) over time. Data are usually recorded in multiple axes.

Acoustic telemetry: telemetry based upon emitted and received sound waves. Used to determine the location of aquatic animals.

Archival loggers: miniaturized data collection devices that are attached to or implanted in animals and store data onboard.

Biologging: measurement of physiological, behavioral or energetic data using archival loggers.

Biotelemetry: remote measurement of physiological, behavioral or energetic data by animal-borne sensors; typically excludes measurement of animal location data alone [46].

Duty cycle: a method of conserving battery life in AVEDs by programming systems to turn off in response to specified variables, such as behavior.

Onboard storage: video data is captured and stored digitally on an AVED, accomplished by using an SD card, flash card or hard drive connected to the system.

Radio telemetry: transmission of information by radio waves. Often used to determine the location of terrestrial animals; can also include collection of physiological data.

Radio tracking: the technique of obtaining data about an animal through the use of radio signals from or to a device carried by the animal. There are three types of radio tracking used today, including very high frequency (VHF), global positioning system (GPS) and satellite tracking.

Time-depth recorder (TDR): a device commonly deployed on marine animals that records and stores depth data over time.

Transmission-based system: video data are transmitted in real time from an AVED through an antenna to a computer for download and storage. In open habitat, video can be transmitted up to 5 km (3 miles).

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Box 1. Technology in progress: the animal-borne video system

AVEDs have progressed significantly since their advent in 1987, and technological advancements are likely to be rapid over the next decade. The first AVEDs, described by Greg Marshall, were deployed on loggerhead (*Caretta caretta*) and leatherback (*Dermochelys coriacea*) turtles [47]. His work progressed into National Geographic's 'Cittercam', the flagship AVED for marine research [48]. The Cittercam has since decreased in size and weight (Figure 1a), enabling deployment on smaller species, such as the emperor penguin *Aptenodytes forsteri* [3]. Other research teams have independently developed AVEDs for ecological investigations for many species, including horseshoe crabs *Limulus polyphemus* [44], Weddell seals *Leptonychotes weddellii* [2], white-tailed deer *Odocoileus virginianus* [37] and great cormorants *Phalacrocorax carbo* [29].

AVED specifications are driven by study species and research questions. Requisites include a secure animal attachment technique, a video camera, a recording medium, a power source and a reliable method for system retrieval. Attachment methods depend on study species; epoxy glues are used on animals with thick fur [2], animal harnesses are suitable for smaller aquatic animals and birds [3,29], suction cups are appropriate for animals with a tough outer carapace,

such as turtles [49], and clamps secure AVEDs on marine species with large fins, such as sharks [33]. Once attached, AVEDs begin recording at a preset time or are programmed to record in response to an environmental cue that is monitored by a system sensor (e.g. light intensity [37]). Video is then captured continuously [37] or recorded at prescribed intervals [14] and the total system lifespan is ultimately limited by storage space and battery power. Early AVEDs were analog systems that recorded on tape; today digital systems are commonly used, and new hard drive AVEDs hold promise for increased video storage capacity [36]. Transmission-based systems are available [37], but are restricted to terrestrial systems and are far less common than onboard AVEDs. Transmission-based systems are limited by range and signal attenuation, especially in forested or mountainous terrains. Battery power is often supplied by lithium-ion battery packs and is influenced by additional sensors and system features (Figure 1b), such as infrared lights for night vision. Following attachment and data collection, AVEDs are retrieved either by animal recapture [37] or automatic release coupled with a VHF transmitter and acoustic tracking [33]. Once retrieved, video and data from other sensors are downloaded for analysis and AVEDs are often reprogrammed and re-used.

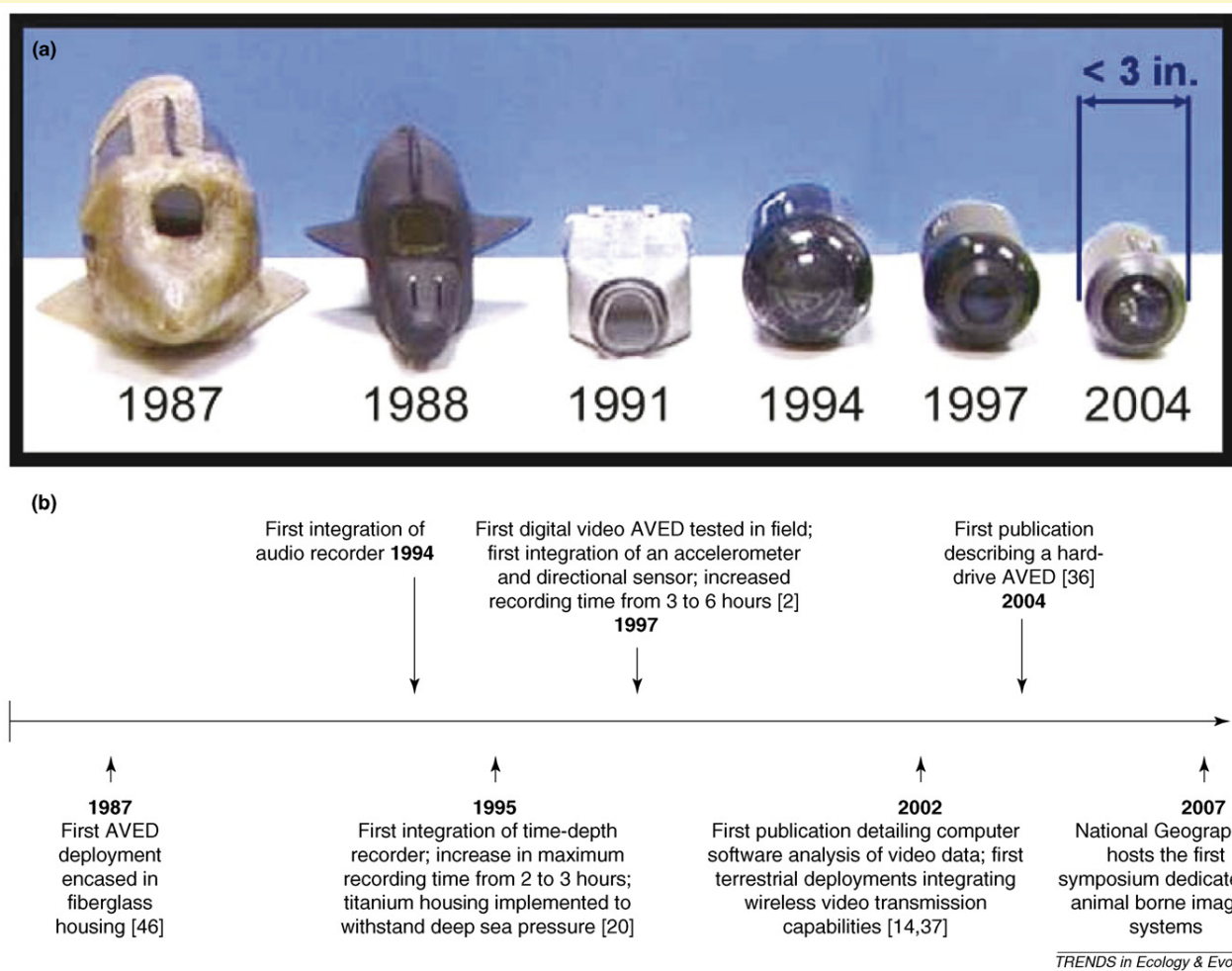


Figure 1. The evolution AVED specifications. (a) The size and weight of National Geographic's Cittercam has decreased over time. (b) The timeline of major advances in AVED technology. Unreferenced advances in timeline were retrieved from <http://www.nationalgeographic.com/cittercam/about.html>. Reproduced with permission from G. Marshall.

addressing conservation questions that AVEDs have helped to answer. We conclude with a discussion of the challenges and limitations of AVEDs and suggest that they are best used as part of a holistic, hypothesis-driven research approach.

Ecological research using AVEDs

The benefits of video data can be shown by looking at the contributions to fine-scale behavioral hypothesis testing, bioenergetics and animal conservation provided by recent AVED studies.

Table 1. AVED specifications by study species^a

Research species	System weight ^b	System size	Other sensors	Attachment method	Other features	Refs
African lion <i>Panthera leo</i>	1.6 kg (NR)	6.7 × 14.9 × 11.6 cm		Neck collar	Automatic release; infrared; transmission-based	UNP
Emperor penguin <i>Aptenodytes forsteri</i>	1 kg ^c (4%)	9 × 25 cm ^d	TDR	Harness		[3]
Great cormorant <i>Phalacrocorax carbo</i>	240 g (9%)	10 × 5 × 4 cm		Harness		[29]
Green turtle <i>Chelonia mydas</i>	2 kg ^c (<4%)	10.1 × 31.7 cm ^d	TDR; sonic transmitter	Epoxy glue	Automatic release	[6,19]
Harbor seal <i>Phoca vitulina</i>	2 kg ^c (<2%)	10 × 25 cm ^d	TDR; temperature sensor; hydrophone	Epoxy glue	Video activated by saltwater	[74]
Hawaiian monk seal <i>Monachus schauinslandi</i>	1.1–2 kg ^c (NR)	10 × 35 cm ^d ; 7.5 × 25 cm ^d	TDR	Glue		[20,23,26,69]
Horseshoe crab <i>Limulus polyphemus</i>	NR	NR	Microsuction optic nerve electrode	NR		[43,44]
Leatherback turtle <i>Dermochelys coriacea</i>	2 kg ^c (<1%)	10 × 30 cm ^d	TDR	Suction cup	Automatic release	[49]
Tiger shark <i>Galeocerdo cuvier</i>	2–4.5 kg ^c (NR)	10.1 × 31.7 cm ^d ; 8.8 × 25.4 cm ^d	TDR; temperature sensor; VHF and ultrasonic transmitters	Dorsal fin clamp	Automatic release	[1,33,42]
Weddel seal <i>Leptonychotes weddellii</i>	NR ^c (NR)	13 × 35 cm ^d	Accelerometer; pressure transducer; water speed sensor; compass bearing sensor; hydrophone	Rubber cement and glue	Infrared LEDs	[2,8,13,36]
White-tailed deer <i>Odocoileus virginianus</i>	2.1 kg (<3%)	Camera: 2.2 × 6.9 cm ^d ; transmitter: 3 × 1.5 × 0.3 cm		Attached to antlers or neck collar	Light-activated; transmission-based	[37]

^aAbbreviations, NR, not reported; TDR, time depth recorder; L, length; D, diameter; UNP, unpublished data from G. Marshall; VHF, very high frequency.

^bValue in parenthesis is approximate system weight relative to study animal.

^cDry weight; systems reported to be neutrally or slightly positively buoyant underwater.

^dFusiform or tubular in shape (size listed as diameter x length).

Table 2. Applications, advantages and disadvantages of animal-borne sensors recording location, imagery or sound^a

Method	Applications	Advantages	Disadvantages	Refs
Acoustic recording	Animal communication and behavior	Records animal vocalizations and environmental stimuli	Might be difficult to interpret animal vocalizations without visual or location data	[2,14]
GPS sensors	Animal space use, including habitat use and animal movements	On-board storage eliminates manual tracking; higher frequency of observations than telemetry; often highly accurate	Variable accuracy and recording rates across habitats; often requires correction factors; size limitations of sensors; costly	[54,56]
Satellite telemetry	Large-scale animal movements (e.g. migration)	Long-range transmission capability; ability to collect high number of locations; does not require manual tracking	Less accurate than acoustic and radio telemetry or GPS sensors; only provides large-scale movements; costly for tags and recording data	[54,55]
Still images	Behavior; habitat use; animal interactions; presence-absence	Provides information for rare and elusive species; relatively inexpensive and lightweight	Discontinuous accounts of behavior can be difficult to interpret; limited by battery life, data storage, system weight, trigger times, resolution and robustness of apparatus	[61]
Time–depth recorder	Underwater vertical movements of marine animals	Generates reliable depth data at high resolution (often >1 measurement per second); small sensors can be applied to many species	Behavior must be inferred from depth data; only provides data on vertical space use	[59,60]
Telemetry	Habitat use, animal movements, demographics and physiology	Generates location data; can be highly accurate (e.g. <5 m) for some taxa in certain environments; common method with broad literature base; transmitters have become very small; widely available	Behavior must be inferred from location data, which can be unreliable owing to tracking errors; costly in personnel time	[52,57,62]
Video (AVED)	Behavior; habitat use, animal interactions; foraging ecology; energetic output; reproduction	Captures detailed accounts of animal behavior; provides context for other sensor data; offers a perspective from the view of the animal	Systems are large and limited by battery life, data storage and cost; not commercially available; small sample sizes are common; terrestrial systems susceptible to damage and lens obstruction	[2,29,37,44,48]

^aFor a comparison of biotelemetric physiological sensors, see Ref. [46].



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Figure 1. AVEDs in use for ecological research. (a) An AVED captured the underwater hunting tactics emperor penguins *Aptenodytes forsteri* beneath Arctic sea ice [3]. (b) A robotic model of the lateral eye of a horseshoe crab *Limulus polyphemus* was created from data collected from an AVED equipped with a microsuction electrode that measured optic nerve activity [44]. (c) AVEDs were used to examine food selection choices of white-tailed deer *Odocoileus virginianus* [37]. (d) Crittercam deployed on an African lion to record behavior. (e) Still frame from a Crittercam attached to a Hawaiian monk seal *Monachus schauinslandi* as it encounters a shark. (f) Still frame from a Crittercam attached to an adult African lion *Panthera leo* showing a lion cub feeding on a zebra *Equus* sp. carcass. (g) Still frame from an AVED attached to a white-tailed deer *Odocoileus virginianus* showing an adult female drinking from a pond. Reproduced, with permission, from (a) Ref. [44]; (b) Ref. [44]; (c) Ref. [37]; (d–f) G. Marshall; and (g) University of Missouri and Missouri Department of Conservation research group.

Box 2. Comparing animal-borne sensor, location and imagery technologies

Animal-borne sensors can collect diverse data, including location information from telemetry; physiological data; motion patterns (from an accelerometer); estimates of proximity to other animals; temperature and depth for aquatic animals; still images; and video (Table 2). Other reviews [34,46,50,51] discuss physiological sensors in biotelemetry studies.

Although the collection of animal location data is often limited by logistical constraints (e.g. manual tracking), error in location estimates (owing to animal movement and terrain [52–56]) and cost (i.e. satellite and GPS systems [54]), such data answer many research questions regarding animal behavior, space use and population demographics [52] (Table 2). Furthermore, telemetry can provide highly accurate location data for some taxa in environments that allow fine-precision tracking (e.g. fish in coastal waters [57]). However, without knowledge of ‘why’ the animal was observed at a particular location, it becomes difficult to ascertain the importance of the location [58]. Similarly, time-depth recorders (TDRs) can identify important habitats and threats (e.g. traffic of ships and other vessels) for aquatic species, and are now small enough to be used on animals <200 g (e.g. Ref. [59]). However, more than one behavior sometimes results in similar TDR patterns, making interpretation difficult (e.g.

Ref. [60]). Still imaging and AVEDs both offer context that is often necessary for interpretation of location data and can correct data from other sensors.

Animal-borne video or still imagery are most appropriate for elusive species in inaccessible environments (e.g. deep-diving marine species) and for fine-scale assessments of animal behavior (e.g. food selection [37]) and species interactions. For example, still cameras recently captured the first evidence of group foraging behavior for emperor penguins *Aptenodytes forsteri* [61]. However, unless the interval between images is small (e.g. <10 s), it can be difficult to piece together animal behavior in these snapshots of activity because important detail could be lost. Still images might also provide insight into habitat use if sampling schemes are well-designed. Video can clarify fine-scale behaviors, such as reproduction, social behavior and foraging (e.g. Ref. [48]) and can correct data from other sensors. For example, AVEDs revealed that several individual tiger sharks *Galeocerdo cuvier* were using shallow habitats over twice as much as was estimated by acoustic tracking methods [33]. For most species, AVEDs can incorporate limited number of additional sensors owing to weight limitations associated with increased power requirements (i.e. more batteries).

Behavioral studies: generating and testing fine-scale hypotheses

Human observation, inferences made from physiological sensors and images collected by stationary cameras provide invaluable data about animal behavior. However, these techniques have generated relatively little data on many elusive species, such as deep-diving marine animals. For these species, the lack of basic behavioral data makes it difficult to test, or sometimes even specify, behavioral hypotheses. For example, mouth and gut analyses suggest that carnivorous juvenile green turtles *Chelonia mydas* become herbivorous during adulthood, but there is little consensus among studies [5]. AVEDs revealed green turtles feeding on jellyfish and ctenophores more than expected, identifying animal matter as a more important food source for adult turtles than previously thought [6].

AVEDs not only help examine fine-scale hypotheses, but can also stimulate future work by providing a foundation of descriptive, life-history data from which researchers can build focused hypotheses. For example, data on the behavior of midwater fishes is scarce, largely owing to the difficulty of observing free-ranging populations. Previous trawl catch data recorded adult Antarctic toothfish *Disostichus mawsoni* occurring at depths of 300–500 m [7]. However, observations from AVEDs attached to Weddell seals *Leptonychotes weddellii* suggest that they are common at depths of <200 m and, similar to Antarctic silverfish *Pleuragramma antarcticum*, might migrate in response to changing environmental conditions, such as light intensity [8]. These fish species are important prey for whales, seals, other fishes and seabirds and thus their impact upon the Antarctic marine food web is substantial. Drawing conclusions about the distribution of prey at the population level from the back of a predator carrying an AVED should be viewed cautiously; however, such data can generate hypotheses and stimulate future research into the environmental conditions that govern animal abundance and movements.

AVEDs can also reveal fine-scale interactions between animals and their environment. To keep their carapaces free from algae and organisms, green turtles engage in symbiotic relationships with cleaner fish in reef habitats (e.g. Ref. [9]). However, turtles in habitats dominated by sea grass or sand lack access to these species, leading researchers to hypothesize that they clean their carapaces by other means. AVEDs revealed that green turtles adapted to such habitat by cleaning themselves on underwater sponges and rocks [6]. Previous research into green turtle dives has not revealed this self-cleaning behavior and rubbing behavior is likely to be misclassified as foraging in time-depth recorder (TDR) datasets [10,11]. Patches of sponges and rocks, therefore, might be an important, overlooked habitat component. Knowledge of these fine-scale interactions often is necessary for understanding the importance of micro-habitat selection.

Energetic studies: benefits of integrating AVEDs with other sensors

AVEDs have the greatest potential for explaining ecological mechanisms when video is integrated with other animal-borne sensors, because data can then be interpreted within

the context of animal activity. Understanding the energy budgets of animals is important for predicting their survival in different habitats. For example, the potential of an organism for invasion can be reflected in its ability to maintain a net positive energy balance under a variable set of environmental conditions (e.g. Ref. [12]). Yet few field experiments have quantified animal energetics because of the difficulty of simultaneously measuring metabolic rates, energy expenditure and animal behavior without affecting behavior.

Like any predator, predatory marine mammals must balance the high energy costs of hunting with the energy gain of prey capture. Precisely how they do this is often poorly understood. In Weddell seals, AVEDs showed that swimming costs increased linearly with the number of strokes taken, and prey intake and digestion increased the post-dive oxygen recovery by 44.7%, suggesting that there is a trade-off for the seals between the duration of hunts and the associated potential energy gain [13]. Similarly, AVEDs revealed that harbor seal *Phoca vitulina* hunting tactics depend on prey visibility and that seals swim faster and spend more time pursuing and handling cryptic prey than conspicuous prey [14]. If energy intake from prey ingestion is not sufficient to offset the costs of hunting, a negative net energy balance can result and, over time, seal survival can be compromised [13]. By using AVEDs to quantify the energetic requirements of foraging and the profitability of prey species, researchers can build models to predict the prey abundance, species composition and distribution necessary to sustain a population of top predators in an ecosystem.

Similarly, behavioral adaptations are crucial for enabling oxygen-limited marine species to perform deep dives. Marine mammals conserve energy and maximize oxygen use by traveling within a narrow range of speeds while submerged [15]. However, many species routinely perform deeper dives than predicted from their aerobic metabolic rates, suggesting that they have behavioral adaptations beyond efficient travel speeds [16,17]. AVEDs recorded changes in locomotor behavior during dives in four species: the Weddell seal, the northern elephant seal *Mirounga angustirostris*, the bottlenose dolphin *Tursiops truncatus* and the blue whale *Balaenoptera musculus*, revealing that energy-saving locomotory changes (i.e. prolonged gliding) throughout dives were similar for all species [18]. This provides evidence for convergent evolution of swimming strategies to mitigate the common constraint of limited oxygen supply during dives in pinnipeds and cetaceans, despite considerable differences in body shape and propulsion technique. AVEDs also revealed that green turtles adjust their locomotor effort in response to changes in buoyancy during dives, further suggesting that swimming behavior has a central role in optimizing energy use in marine species [19].

Contributions to conservation

Much recent AVED work has focused on the largest remaining colony of endangered Hawaiian monk seals *Monachus schauinslandi* near Hawaii, the population of which has declined substantially. Critical oceanic habitat designated by the US Department of Commerce was limited to depths <40 m; AVEDs revealed adult male seals foraging almost exclusively on oceanic terraces and slopes

at depths >40 m, including sites of commercial fishing operations [20]. Previous scat analysis studies might have underestimated the take of commercially fished species (e.g. lobster) owing to bias caused by differential digestion of animal matter [21,22], whereas AVEDs provide robust foraging data. Shortly after the AVED study in 2000 [20], a US Federal Court ruling closed lobster and bottomfish fisheries in the surrounding region, charging the fisheries with a violation of the Endangered Species Act by failing to assess the impacts of harvest on monk seals (US District Court of Hawaii Civil Case No. 00–00068SPKFIY).

Conservationists are also concerned that commercial harvest of precious pink (*Corallium* sp.) and gold (*Gerardia* sp.) coral near Hawaii destroys habitat used by monk seals. Telemetry and TDR studies have documented seals occasionally performing dives deep enough to encounter coral beds, but they have not described behavior during such dives [22]. Although AVEDs did not document seals using precious coral beds, they showed them foraging for fish in beds of black coral *Cirrhopathes* sp., suggesting that precious coral beds might also be used by monk seals [23]. Despite its small sample size ($n = 5$), this study serves as an indicator that coral harvest might have an impact on monk seal foraging and highlights the need for further research.

The emaciation and poor survivorship that characterizes juvenile monk seals is suspected to be related to prey availability [24] and oceanic conditions (e.g. El Niño events [25]), but the exact mechanisms are not fully understood. AVEDs recorded yearling seals foraging in oceanic sand fields on populations of flounders (Family Bothidae), which are especially susceptible to changes in oceanic regimes; this suggests that managing for these prey during unfavorable oceanic conditions might increase the survival of juvenile monk seals [26]. In both of these AVED studies [23,26], video data provided information that other methods had not captured, enabling researchers to link foraging behavior and prey selection with fine-scale habitat use to understand more fully the dynamics of seal movements, prey availability, foraging behavior and microhabitat selection.

In another example, fine-scale data provided by AVEDs helped resolve a perceived human–wildlife conflict. The predation of fishes by populations of European great cormorants *Phalacrocorax carbo sinensis* and American double-crested cormorants *Phalacrocorax auritus*, which have grown rapidly in recent years, is viewed as a threat to commercial fisheries [27,28]. In addition, fishers claimed that unsuccessful foraging attempts by cormorants regularly injure fish, decreasing their market value. Video from AVEDs and dive tank-mounted cameras revealed that this non-lethal damage is negligible and that cormorants rarely injure prey without capturing it (e.g. 0.4% of cases in double-crested cormorants) [29]. These data help refute claims that cormorants have widespread impact upon the economic gain of commercial fisheries by injuring fish.

AVEDs have served as a vehicle for public outreach and education, which sets the stage for conservation by garnering public support and providing a framework of ecological knowledge. To be relevant, conservation education should frame scientific data in context [4] and should stimulate the public's imagination [30]. AVEDs facilitate imaginative

education of ecological processes by providing intimate views from undisturbed animals in their natural surroundings. For example, several of the same video segments that provided data in our examples are available to the public on websites that also include information about the ecological role and conservation status of the species (<http://channel.nationalgeographic.com/channel/crittercam>).

Identifying challenges, limitations and developmental needs

Despite the utility of AVEDs in conducting behavioral, energetics and conservation-related research, several obstacles must be addressed to realize their full potential. A foremost challenge facing AVEDs is the assumption that systems do not compromise the natural behavior of an animal or induce harmful levels of stress (Box 3).

Sample size issues

As with early telemetry research, AVED studies have suffered from small sample sizes (i.e. n often <10). There

Box 3. Evaluating the effects of AVEDs on animal behavior and well-being

If research equipment affects the natural behavior of an animal, study results can be biased and the impact on the animal might be ethically unacceptable. Reviews of studies of telemetry transmitter effects suggest that tags should be <3–5% of animal body mass, but smaller percentages are recommended for birds and aquatic animals [62–64]. External tags on aquatic fauna should be <1–2% of body mass and fusiform or cylindrical shapes are recommended to minimize hydrodynamic drag [48,65,66]. Drag caused by tags can now be modeled using computer simulations [67], enabling optimization of tag design without conducting wind or water tunnel experiments (e.g. Ref. [68]). We encourage collaboration between ecologists and engineers to minimize the impact on animals.

AVEDs have a greater potential to affect animals than other technologies (e.g. telemetry transmitters) because they are larger, heavier and cannot be implanted subcutaneously. Several studies have quantified animal response to AVED attachment [3,14,29,33,69]. For example, maximum dive depth, dive duration, average descent rate and average ascent rate did not differ in pre- and post-AVED attachment measurements in Hawaiian monk seals *Monachus schauinslandi*; however, the sample size was small ($n = 10$) and the samples showed considerable variation [69]. The large size of many AVED study species (e.g. seals) has limited the impact of AVEDs; smaller animals are likely to show more discernible responses. Of all AVED assessments, the only reported deleterious effect is for a relatively small species, the emperor penguin *Aptenodytes forsteri*; individuals showed a 21–35% decrease in the duration of foraging trips while carrying an AVED [3].

A recent call for an ecological analog to the bioethics field in medicine [70] highlights the importance of measuring and minimizing the effects of AVEDs on animals [71]. AVED research perhaps faces greater scrutiny from the public than do other animal-borne sensors owing to the charismatic nature of test subjects (e.g. lions *Panthera leo*), the media coverage associated with AVEDs and their growing role in public outreach. Studies should be conducted before deployment to assess the impact of AVEDs, using carefully designed and replicated experiments that compare control and AVED-equipped animals. In addition to demographic and behavioral investigations, we suggest that researchers use physiological assessments, which are currently lacking in AVED research, to quantify effects. Non-invasive procedures, such as fecal glucocorticoid metabolite assessment, do not require repeated handling of study animals and are a sensitive measure of stress [72,73]. Unless some attempt has been made to understand impact, study results should be viewed with caution.

are now guidelines for sample sizes for telemetry research (e.g. Ref. [31]), but similar protocols for AVEDs are lacking, leaving researchers to derive sample size from personal knowledge or common practice. To overcome this challenge, we suggest that researchers ask focused ecological questions (e.g. what is the foraging success of age and sex class x of species y for prey species z ?) and conduct pilot experiments to estimate the variation of desired parameters, which can lead to sound guidelines for necessary sample sizes. As in telemetry studies [32], AVED researchers should expect high variation in individual behavior depending on age, sex and local habitat characteristics. When researchers cannot respond by deploying a large number of AVED systems, they need to focus on specific conditions to gain reliable insights into fine-scale mechanisms and use additional study, theory and modeling to scale these insights up to broader conditions.

AVEDs are not commercially available, which restricts access for most researchers. The available units are mainly custom-built or are only available to researchers on loan for short time frames. For some studies requiring high samples sizes (e.g. foraging), the lack of access to AVEDs is disadvantageous. Thus, AVEDs might not offer more information than can be obtained through traditional approaches and could be reduced to anecdotes for animals that do not forage frequently (e.g. sharks). With plummeting prices of video and battery technology, it is now possible to build units that could be purchased and used over the time frames necessary for ecological studies, thus providing a way to increase sample sizes. For example, it can be difficult to obtain large sample sizes for telemetry-based habitat use studies on wide-ranging species (e.g. sharks) because of the labor requirements of manual tracking; AVEDs can increase sample size for such studies because they provide habitat use data without requiring tracking [33]. Many other animal-borne technologies have been successful because they are commercially available, and we encourage the commercial development of AVEDs.

Battery power, system weight and storage capacity

The lifespan of an AVED is contingent upon the size, weight, storage capacity and battery power of the system. The size and weight of AVEDs have decreased over time (Box 1). Larger species, such as seals, can carry larger systems and have therefore been the focus of early AVED research, although AVEDs have been deployed on animals weighing <5 kg (e.g. horseshoe crabs *Limulus polyphemus*, Figure 1b). Biotelemetry research was similarly focused on large species during its infancy [34], and yet there is now an external heart rate transmitter designed for small birds and bats that weighs <1 g [35]. Commercial digital video cameras not much larger than postage stamps are currently available (e.g. <http://supercircuits.com>), but adapting them into field-worthy AVEDs will take time, and there are trade-offs between system size and system lifespan; smaller systems mean fewer batteries, less onboard storage and, ultimately, shorter system lifespan. As AVEDs become smaller and more species become candidates for AVED research, ecologists should collaborate with engineers to ensure system lifespan is maximized by optimizing energy use and video storage.

Onboard storage capabilities have advanced only marginally in the past ten years, but recently developed hard-drive video cameras have increased storage capacity from 6 h [2] to over 80 h [36]. Transmission-based terrestrial AVEDs are limited predominately by battery power rather than data storage because video can be transmitted to a remote downloading station [37] (Figure 1c,d). It is also crucial to incorporate video compression to maximize storage capacity; a duty-cycled system with advanced video compression and a large onboard hard disk could record months of data in the field, provided there is sufficient power. Systems can also be designed to transmit stored data wirelessly to downloading stations placed in locations frequented by animals, thereby releasing the onboard storage disk space. Similarly, packets of video data can be relayed through transmission nodes placed throughout the habitat of an animal, creating a network through which data can travel, with a computer as the terminal destination [38].

At this point, advancements in storage seem to be outpacing reductions in power consumption, making battery power and battery weight the major technological factors limiting AVEDs. Alternative battery sources, such as solar-powered or motion-recharged batteries, hold promise, but the immediate solution lies in designing intelligent systems that power off during specific behaviors by using animal-borne sensors (e.g. accelerometers). Research objectives requiring lower quality video might also lengthen battery life through reductions in video quality (e.g. lower frame rate).

Efficient analysis of video data

AVED researchers must analyze enormous amounts of data efficiently. So far, analysis has been carried out primarily by visual inspection by wildlife experts (e.g. Ref. [37]), although computer software that categorizes and quantifies specific behaviors has aided some studies (e.g. Ref. [14]). Semi-automated software analysis of video data is an indispensable element of AVED technology. Important applications include: (i) image stabilization for more efficient visual analysis; (ii) scene classification that organizes and quantifies video segments based upon specified behaviors, movements [39] or sensor data (e.g. temperature); (iii) species-specific face detection algorithms [40]; and (iv) for AVED networks operating on populations of animals, analysis of data packet transmission history. In the case of (iv), software can be used to categorize video segments based on the presence or absence of other AVEDs within transmission range, thereby enabling researchers to focus on video segments in which animal interaction is likely [41].

Conclusions and future directions

AVEDs contribute to behavioral research, physiological studies and animal conservation by integrating video recordings of animal activity from the perspective of the animal (Figure 1e–g) with other animal-borne sensor data. As the challenges described here are addressed, AVED research should evolve from small-scale, individual-focused studies to long-term investigations of populations. With AVEDs come many research opportunities, but research questions and techniques will have to coevolve

with the technology to ensure that the contributions of AVEDs to ecology and conservation are maximized and efficient. AVED technology must also become more widely accessible to the scientific community through commercialization of this technology.

As with all novel technologies, there is a temptation to deploy AVEDs before research questions are clearly identified. For example, early telemetry research included many descriptive case studies without a clear idea of whether the question was important or whether data would be sufficient to answer it. Many early AVED studies have been descriptive in nature and have provided a foundation of basic knowledge upon which future experiments can be designed. Such studies have value for elusive species about which we know little. However, as in early telemetry studies, a large number of exploratory studies had value and were publishable; but their efficiency in building scientific knowledge would have been higher had study questions been more mechanistic, with less emphasis on their novelty and descriptive nature. Several studies have used AVEDs to evaluate *a priori* hypotheses and thus have made fuller use of the technology (e.g. [20,23,29,42]). Proof-of-concept pilot studies and even data from related species or those with similar niches can be useful for developing meaningful hypotheses.

We encourage ecologists to implement AVEDs to answer research questions and management issues that cannot be addressed using traditional methods. We envisage future applications including research into animal interaction [43,44] and disease transmission (e.g. by establishing contact rates between animals for spread of chronic wasting disease), explaining mechanisms for rare events or behaviors (e.g. tool use in New Caledonian crows *Corvus moneduloides* [45]), mitigating human–wildlife conflicts (e.g. reducing animal–vehicle collisions through study of road-crossing behavior) and continued research into factors influencing the survival of endangered species. AVEDs are especially suited for testing hypotheses about fine-scale behavior, and they are most effective as part of a system to capture many forms of data simultaneously.

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