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Review

Distinguishing technology from biology: a critical review of the use of GPS telemetry data in ecology

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In the past decade, ecologists have witnessed vast improvements in our ability to collect animal movement data through animal-borne technology, such as through GPS or ARGOS systems. However, more data does not necessarily yield greater knowledge in understanding animal ecology and conservation. In this paper, we provide a review of the major benefits, problems and potential misuses of GPS/Argos technology to animal ecology and conservation. Benefits are obvious, and include the ability to collect fine-scale spatio-temporal location data on many previously impossible to study animals, such as ocean-going fish, migratory songbirds and long-distance migratory mammals. These benefits come with significant problems, however, imposed by frequent collar failures and high cost, which often results in weaker study design, reduced sample sizes and poorer statistical inference. In addition, we see the divorcing of biologists from a field-based understanding of animal ecology to be a growing problem. Despite these difficulties, GPS devices have provided significant benefits, particularly in the conservation and ecology of wide-ranging species. We conclude by offering suggestions for ecologists on which kinds of ecological questions would currently benefit the most from GPS/Argos technology, and where the technology has been potentially misused. Significant conceptual challenges remain, however, including the links between movement and behaviour, and movement and population dynamics.

Keywords: Argos; movement; habitat selection; GPS technology; survival; demography

1. INTRODUCTION

In the 1960s, the Craighead brothers pioneered the first use of radiocollars to study terrestrial wildlife when they radiocollared the first grizzly bears and elk as part of their groundbreaking studies in Yellowstone National Park (Craighead 1982; Craighead *et al.* 1995). Since then, ecologists have adapted their technology across the world to study the ecology and distribution of terrestrial and aquatic species in ways that the Craigheads would have had a hard time predicting. Today, almost 50 years later, a new revolution is underway. With the advent of animal-borne technology such as GPS or Argos collars, tags and transponders, ecologists are now taking the next step to understanding animal ecology in a detail never envisioned by the Craigheads. Today, ecologists sitting at their desk can check the movements of even the most difficult to study species such as GPS radiocollared wildebeest (*Connochaetes taurinus*) or Argos-tagged bluefin tuna (*Thunnus thynnus*) on Google Earth, as they check their morning email with minute-by-minute data streams.

Buried under a growing mountain of data comprising millions of locations, it seems a fair time for ecologists to pause and ask the question: what insights into ecology and conservation has all this extra technology really provided us with? Are we really better able to conserve species than with the Craighead's 'primitive' VHF data? And, given the increasing demands on our finite world, what conservation goals are being furthered by our slavish addiction to GPS or Argos technology? Many of the other papers in this special issue of the *Philosophical Transactions of the Royal Society* address the advances in the field of ecology that are being wrought through the application of GPS-based location data (Cagnacci *et al.* 2010). The explosion of such technology is being followed by the development of increasingly sophisticated and quantitative methods to analyse these data (Morales *et al.* 2004; Moorcroft & Lewis 2006). With larger datasets, come increased statistical headaches such as the quantification of GPS bias (Frair *et al.* 2010), appropriate statistical modelling of highly correlated data (Fieberg *et al.* 2010) and debates over the appropriate movement modelling approaches (Bartumeus *et al.* 2002; Smouse *et al.* 2010). One thing that is

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One contribution of 15 to a Theme Issue 'Challenges and opportunities of using GPS-based location data in animal ecology'.

common among all recent papers using GPS or Argos data is the oft-heard statement that understanding movements of animals at fine scales will undoubtedly improve our ability to understand animal ecology and conservation.

Here, we attempt to provide a review of the frequent claim that GPS technology will improve the ability of ecologists to understand animal ecology and conservation. Our goal is to review the advantages and disadvantages of GPS/Argos technology, highlighting its most significant contributions and where it has potentially been misused. We focus first on what we see as the five key limitations of GPS technology. Building on this, we summarize the obvious benefits of GPS/Argos technology, and then review the five major areas in which GPS and Argos technology has really benefitted ecology and conservation. Sifting through these points, we attempt to summarize areas where GPS and Argos technology offer the most useful insights to ecologists. We focus on GPS-based systems, recognizing that while historically Argos has been important especially in marine systems, its lower precision is today being replaced by systems that combine GPS positioning with Argos (or other satellite)-based data retrieval (we call these GPS/Argos systems, see Tomkiewicz *et al*. 2010). Finally, we conclude by offering a prospectus of three major conceptual challenges that would make a major contribution to unleashing the real power of GPS technology to advancing our understanding of animal ecology and conservation.

2. MAJOR DISADVANTAGES OF GPS TELEMETRY DATA IN ECOLOGY

(a) *Cost*

While GPS technology reduces the human resources costs associated with manually obtaining locations, it has come so at the additional and substantial cost of investment in the GPS unit itself. Average costs for GPS collars for ungulates or terrestrial carnivores, for example, range from around USD 2000 to 8000, depending on the features of the collar, battery size, longevity, programmability, remote data access via UHF or satellite communication, etc. GPS/Argos collars have the additional expense of satellite contracts to transfer data, which increase prices proportionate to sampling frequency. Thus, GPS collar costs are an order of magnitude greater than average costs for VHF collars, often in the range of USD 200–600 (Tomkiewicz *et al*. 2010). Despite this disadvantage, costs per GPS unit are already declining as expected with new technology, and we envision a future where researchers can afford to deploy many more GPS units than at present, alleviating some of the following disadvantages.

(b) *Small sample sizes and poor population-level inference*

The high cost/GPS unit has had an unintended influence on sample sizes used in ecological studies because of the trade-off between the number and cost of GPS units. Researchers must often opt for fewer GPS units over a greater number of VHF units, unwittingly sacrificing robust population-level inferences. For example, Lindberg & Walker (2007) provide one of the reviews in the literature of the effects of this trade-off between GPS and VHF units in survival studies. They conclude that more than 20 animals are needed to make reliable statistical inferences about simple comparisons between two populations, and more than 75 for realistically complex studies (Lindberg & Walker 2007). In the study of animal home ranges, Börger *et al*. (2006*b*) similarly argue for a greater number of animals as the sample unit instead of more data/GPS unit. Statistical recommendations from earlier studies should not be ignored in favour of smaller sample sizes of GPS units. For example, for studies of animal survival with known-fate collar data (GPS or otherwise), more than 50–100 animals are needed (Murray 2006). Costs of 50–100 GPS units would currently be prohibitive for survival studies, which is why most researchers still use VHF units to estimate survival (table 1). For studies of resource selection, sample size requirements of more than 30 units for robust population-level inferences likely still apply (Leban *et al*. 2001), resulting in the same trade-off (table 1). These recommendations do not address representativeness of the sample, which is a function of the total size of the population (i.e. 30 individuals sampled out of 300 versus 300 000). Thus, regardless of the costs of GPS technology, ecologists should heed general practices of good study design and should ensure that an appropriate number of GPS units are deployed if population-level inferences are the goal (table 1).

We argue that the trade-off between cost and sample size of GPS telemetry studies has led to inappropriate use of this technology by drawing ecologists into accepting lower sample sizes than would be possible using VHF units. We conducted a survey of recent (last 5 years) studies of terrestrial wildlife (including our own studies) using the keywords ‘GPS’ or ‘VHF collar’ and ‘habitat’ in the *Journal of Wildlife Management, Ecology, Ecological Applications, Journal of Applied Ecology, Wildlife Monographs, Journal of Animal Ecology and Proceedings of the Royal Society B*. We restricted our review to 30 studies that focused on habitat selection and movement to avoid problems of mixing study objectives. Mean sample size of the number of animals in GPS-based studies was $n = 18.1$ (range 4–82) compared with $n = 58.7$ (range 14–188) for VHF-based studies. Ten studies used a combination of GPS and VHF collars in the same study (see next paragraph), and in these paired comparisons, mean GPS and VHF sample size was 13.3 and 58.8, respectively. Clearly, ecologists are trading-off between sample size and expense, but as yet, the inferential weaknesses of this problem have not been addressed. Other examples of inappropriate use occur when researchers use GPS devices when they are not needed. For example, where researchers propose to monitor annual survival (for which detailed time of death is not needed) using GPS devices when VHF units would suffice, an unnecessary waste of limited conservation science funding. A final example of misuse that we commonly see is mistaking increased precision acquired from a limited number of

Table 1. Potential advantages and disadvantages of GPS/Argos technology for addressing major questions/themes in animal ecology and conservation including studies cited in-text and this Theme Issue.

ecological/ conservation question	advantages	disadvantages	citations
resource selection, corridor mapping	increased precision, accuracy, reduced sampling bias; application in difficult to study wide-ranging species	trade-off between sample size and cost/GPS unit may reduce statistical rigour; need to improve measures of resource availability to match fine-scale animal location data	Thirgood *et al.* (2004); Whittington *et al.* (2005); Sawyer *et al.* (2006); Frair *et al.* (2010)
behaviour	application to wide-ranging species who could not previously be studied; numerous statistical methods to discriminate statistical behaviours	lack of information about 'real' behaviour (could be remedied with field observations or animal-borne video or cameras for example)	Davis *et al.* (1999)
migration	ability to study rare rapid migration movements that were frequently missed with VHF studies	trade-off between sample size and cost/collar may reduce statistical rigour	Polovina *et al.* (2001); Littaye *et al.* (2004); Meyburg *et al.* (2003); Mueller *et al.* (2008)
home range	increased precision, accuracy, reduced sampling bias; application in difficult to study wide-ranging species	trade-off between sample size and cost/GPS unit may reduce statistical rigour; union of movement, resource selection and home range dynamics	Moorcroft & Lewis (2006); Kie *et al.* (2010)
demographic studies (e.g. survival, reproduction)	increased precision about timing of mortality and reproduction (e.g. calving sites)	trade-off between sample size and cost/GPS unit may reduce statistical rigour—most present studies still use VHF to ensure adequate sample sizes	Haydon *et al.* (2008); Morales *et al.* (2010)
movement ecology	recent advances in movement ecology have been driven by GPS technology's increased precision and accuracy	trade-off between sample size and cost/GPS unit may reduce statistical rigour; scaling issues remain in separating out the biology of movement from the statistics	Morales *et al.* (2004); Moorcroft & Lewis (2006); Smouse *et al.* (2010)
human–wildlife conflict	increased insights into mechanisms governing human–wildlife encounters and conflict	trade-off between sample size and cost/GPS unit may reduce statistical rigour	Whittington *et al.* (2005); Sawyer *et al.* (2006); Graham *et al.* (2009)
climate change	increased mechanistic insights into climate-movement/habitat/ population links	requires combination with mechanistic studies of impacts of climate change on food webs	Durner *et al.* (2009)

individuals for increased representativeness of the population. Consultants hired by energy development companies in Alberta have argued for oil and gas development in areas with no sampled GPS locations, using the lack of telemetry locations as evidence of absence (F. Schmiegelow 2003, University of Alberta, personal communication). The illusion of precision afforded by GPS technology belies the costly sacrifices made in experimental design if ecologists are deploying insufficient sample sizes for robust population inferences.

Practically, one approach that has been used to attempt to overcome problems of diminished sample sizes is the use of a validation sampling approach. This is where ecologists combine GPS and VHF units (as the paired studies above did), and use the VHF units to validate the resource selection, survival or movement models developed with more fine-scale GPS data (Hebblewhite *et al.* 2008). This approach has proved useful, yet the problems of validating across temporal sampling scales (GPS data 1 per hour versus VHF data 1 per week, for example) remain unclear. In addition, redeploying GPS units on new individuals each year may help achieve required sample sizes for resource selection or movement studies for example, but this approach would fail to address sample size problems for survival studies because mortality is the sample unit, and might mask important annual differences in resource selection.

A related weakness of GPS devices often further reduces sample sizes: collar failure (Tomkiewicz *et al.* 2010). Almost all users of GPS units for wildlife report some level of complete failure, reducing sample sizes and strength of inference even further. This can arise from failure to recover GPS units, or failures of remote-retrieval systems or the technology itself (e.g. Hebblewhite *et al.* 2008). These 'catastrophic' failures can range from 5 to 50 per cent of the GPS units deployed (Gau *et al.* 2004; Hebblewhite *et al.* 2008). In addition to the impact on sample sizes, failures often result in the need to capture and handle additional individuals that precipitates costly and risky re capture (Arnemo *et al.* 2006). Ecologists need to carefully consider the effects of increased costs on basic principles of good study design and ethics of animal capture and handling.

(c) *Overemphasis of the importance of fine-scale data*

Knowing what an animal does every 5 min may give us the potentially false impression that fine spatial and temporal scale dynamics are relevant to ecology or, most critically, conservation. Too often we hear managers claim that fine-scale insights of GPS telemetry will enable them to mitigate forestry or energy development, for example, when the fitness consequences of habitat fragmentation are operating at larger spatio-temporal scales, or when time lags occur between development and population impact. For example, in the case of threatened woodland caribou declines, the bulk of research strongly suggests declines are caused by large spatial scale anthropogenic disturbance that has increased predation (Mcloughlin *et al.* 2005; Wittmer *et al.* 2005; Environment Canada 2009). While there are certainly examples where fine-scale data are of obvious conservation value (e.g. pronghorn migration, see below, table 1), it is not necessarily true in all cases. Ecologically, we argue below that the most difficult problem facing ecologists using GPS data is how to scale-up to the population consequences of movement (Morales *et al.* 2010; Owen-Smith *et al.* 2010). We return to the challenge of scaling below, but caution that fine-scale knowledge does not necessarily equate to fitness insights.

(d) *Divorcing biologists from the field*

The release from manually tracking wildlife is both a blessing and a curse. Instead of getting an important biological 'feel' for what drives animal ecology, ecologists now spend increasingly less time in the field becoming acquainted with their study species and the landscapes they dwell in. While qualitative, we believe this has potential to interact with some of the previously discussed weaknesses of GPS devices, with biologists who have no 'field' sense of what their study population is, how representative their sample of GPS units is of the entire population or the problem of assuming fine-scale movements are relevant. What made the Craigheads' great biologists was that they were field biologists first and foremost, and their keen skills of observing animals in their native environments cannot be substituted with technology divorced from the knowledge of natural history.

(e) *Difficulties relating fine-scale movements and coarse-scale evaluations of resource availability and behaviour*

Finally, the last major problem we see is the mismatch between information about animal movements, their behaviour and their environment. We now have incredibly fine-scale data on animal movements, but lack data at the same resolution (i.e. grain size) about what resources were available to them or their behavioural state in a similarly fine-scale way. Instead, we often build sophisticated models to 'test' between the importance of 'habitat' and other factors driving movements of animals where we pair data on hourly movements with a coarse-grained and static permanent 'map' of landcover resources (Dalziel *et al.* 2008; Frair *et al.* 2010). Ecologists should become better in matching temporally varying estimates of resource availability at the same time scale as animal movements. While a daunting task, such data are available at some finer grain sizes. The availability of fine temporal (8 day) and spatial (250 m^2) remotely sensed data from satellites such as MODIS (Moderate Resolution Infrared Satellite; Huete *et al.* 2002) now provide ecologists with ready information on forage biomass, terrestrial and aquatic net/gross primary productivity, and snow cover that can be matched temporally with GPS data (Huete *et al.* 2002; Running *et al.* 2004; Hebblewhite 2009). Urbano *et al.* (2010) describe sophisticated database management systems to help ecologists link animal and environmental data. The power of coupling of satellite technology on animal movements together with resource availability is self-evident, but, as yet, relatively few studies have attempted to harness it.

This problem is amplified when it comes to behaviour (table 1). Despite sophisticated tools that allow us to statistically distinguish between different movement modes in a GPS movement dataset (Morales *et al.* 2004; Nathan *et al.* 2008; Patterson *et al.* 2008; Schick *et al.* 2008), we only have a nascent idea of what animals were really doing from a behavioural viewpoint. This problem is amplified because our ability to statistically discriminate different movement 'modes' in GPS data is often extremely scale-dependent, i.e. whether we are discriminating movements based on 15 min, 2 h or 24 h data (see also Boyce *et al.* 2010; Owen-Smith *et al.* 2010). Statistically, we now can use a growing array of methods to distinguish between 'slow' and 'fast' movement behaviours. Despite obvious improvements over older VHF telemetry, however, what actual behaviour these statistical states correspond to is still unknown. We see connecting statistical and real behaviour from GPS-based locations as a critical area for new research. Biologists should observe (as best as possible) their study species at the same time as GPS data are being collected to be able to validate the statistical models and connect GPS data to different behaviours. While certain technological advances themselves may help, such as GPS collar-borne remote cameras and other biosensors (Cooke *et al.* 2004), as applied in the famous studies of leopard seal hunting behaviour under the Antarctic shelf ice (Davis *et al.* 1999), we argue that technology should not replace field biology, but be combined with learning from animals in the field, in our efforts to interpreting behaviour and ecology from GPS technology.

3. MAJOR ADVANTAGES OF GPS TELEMETRY DATA IN ECOLOGY

GPS telemetry provides highly precise spatial and temporal location data about animal movements at arbitrarily small time intervals to a degree never before possible with VHF telemetry or other non-invasive methods such as camera trapping or landscape genetics. Our ability to collect data in a manner that is not biased by the ability of human observers to collect it, such as under darkness, during the 24 h winter for polar bears, or on long-distance migrations of ocean-going mammals, is perhaps the strongest advantage of GPS technology. Moreover, GPS precision and accuracy has, especially since the end of selective availability (see Tomkiewicz *et al.* 2010), essentially overcome many of the bias and precision problems posed by VHF or Argos technology. Certainly, animal- and habitat-induced bias remains, but methods to address these remaining issues are increasing (see Frair *et al.* 2010). And now that we can couple GPS with the data-retrieval power of Argos, we can harness the best of both technologies to obtain high precision and temporal resolution data on most medium-sized or large species.

An additional advantage of GPS/Argos technology is freedom from the substantial time investment of manually having to obtain animal locations ourselves. This has reduced the human resources funding required to collect VHF-based location data on species, and obviously reduces human-induced collection bias. This freedom ostensibly gives us more time to collect additional ancillary information about the study species that should help interpret GPS data, for example vegetation, forage or behavioural information. Unfortunately, as we argue below, we feel this opportunity has not been fully exploited, and, as ecologists become divorced from the animals and landscapes in which they live, additional problems arise.

Next, we briefly review five areas where GPS telemetry has benefitted our understanding of ecology and conservation.

4. FIVE EXAMPLES OF REAL BENEFITS OF GPS TELEMETRY-BASED RESEARCH

(a) *Improvements to habitat modelling and conservation*

The advent of GPS telemetry has taken resource selection modelling of habitats important to animals to a whole new level of rigour and ecological understanding. Availability of unbiased, high-quality data on habitat use has undoubtedly improved our ability to identify important habitat for wildlife species and made real contributions to conservation, especially in understanding human impacts on animals. Examples include developing environmental niche models for critical habitat identification using data from 250 GPS-radiocollared endangered woodland caribou (*Rangifer tarandus caribou*) across the entire boreal forest of Canada (Environment Canada 2009); understanding effects of energy development on mule deer (*Odocoileus hemionus*) and caribou (Dyer *et al.* 2001; Sawyer *et al.* 2006, 2009); understanding impacts of human recreation on wide-ranging carnivores (Whittington *et al.* 2005; Hebblewhite & Merrill 2008); and identification of habitat corridors for transboundary conservation of African elephants (*Loxodonta africana*; Graham *et al.* 2009; table 1).

GPS data have also forced biologists to become more sophisticated and, perhaps, honest, in the kinds of ecological questions they ask of animal species when it comes to resource selection and identification of important resources. Instead of collecting ground-based telemetry locations in a biased and non-random fashion, GPS telemetry can provide systematic, highly accurate and relatively unbiased data compared with traditional VHF data collection. Methods to improve and correct for bias in GPS fix-rate, previously ignored in VHF-based telemetry, have become commonplace (see Frair *et al.* 2010). The abundance of finely autocorrelated GPS locations have also forced biologists to develop new solutions to this problem (Fieberg *et al.* 2010). Perhaps, most importantly, GPS telemetry has advanced thinking about defining what is available to an animal. Instead of simply comparing used resources to unused or available resources within some study area or home range (Manly *et al.* 2002), GPS technology has provided the tools for biologists to connect the movement process to more animal-based definitions of what is available at any given time (Fortin *et al.* 2005; Whittington *et al.* 2005; Beyer *et al.* 2010). There is also a growing awareness of the pervasive role of functional responses in resource selection, namely, where selection changes as a function of availability, in numerous recent studies as a result of GPS technology (Mauritzen *et al.* 2003; Osko *et al.* 2004; Hebblewhite & Merrill 2008; Merrill *et al.* 2010).

(b) *Mechanisms of migration*

The study of animal migration provides various examples where the combination of remotely sensed resource availability data with GPS movements have yielded definitive ecological insights (Hebblewhite 2009). Migration has been hypothesized for decades to be a response to spatial variation in food resources, and especially among herbivores such as migratory ungulates, as a response to seasonally pulsed ‘green-waves’ of nutritious forage across large spatial scales (Leimgruber *et al.* 2001; Boone *et al.* 2006; Hebblewhite *et al.* 2008). Similar drivers of marine migration include seasonal pulses of phytoplankton that attract zooplankton and higher trophic levels including pelagic fish predators, sea turtles and the great whales (Polovina *et al.* 2001; Littaye *et al.* 2004; James *et al.* 2005). By combining GPS data on migratory movements of these species with spatially matched resource availability ‘maps’ from MODIS satellites for terrestrial and aquatic forage resources (Polovina *et al.* 2001; Huete *et al.* 2002), clear evidence has been generated for the main hypothesis for migration at scales and across systems that had previously been unthinkable without GPS technology.

(c) *Basic ecology and conservation of wide-ranging species*

Building on the theme of migration, GPS telemetry has enabled significant improvements to our understanding of the ecology of many wide-ranging and difficult to study species. Great advances in our knowledge of basic ecology such as where animals forage, movements and distribution have been made as a result of GPS and Argos technology; sea turtle migration from the Caribbean to the Grand Banks of Newfoundland (James *et al.* 2005); bluefin tuna movements from the Mediterranean to the Atlantic (Block *et al.* 2005); steppe eagle (*Aquila nepalensis*) migration between Asia and Africa (Meyburg *et al.* 2003); wolverine (*Gulo gulo*) movements over a 20 000 km^2 area (Inman *et al.* 2004); migration of barrenground caribou, Mongolian gazelles (*Procapra gutturosa*) and pronghorn antelope (*Antilocapra americana*) over thousands of kilometres (Griffith *et al.* 2002; Berger 2004; Mueller *et al.* 2008); never before documented Weddell seal (*Leptonychotes weddellii*) hunting behaviour (Davis *et al.* 1999); circumpolar movements of wandering albatross (*Diomedea exulans*) (Fritz *et al.* 2003; Weimerskirch *et al.* 2007); and, of course, the global movements of the great whales (Littaye *et al.* 2004). The summary message of all of these studies is that populations of many wide-ranging species move over areas that are orders of magnitude larger in scope than revealed by conventional studies. Conservation benefits of such insights have been legion, with direct implications on harvest management, habitat and movement corridor protection, and transboundary collaboration. In the Serengeti, for example, simple accounting of GPS-based locations in different jurisdictions with different levels of protection highlighted the precarious status of the extraordinary Serengeti wildebeest migration (Thirgood *et al.* 2004). Given advances in technology that are producing ever-shrinking devices, within the next several decades we can expect that GPS technology will reveal the migratory ecology of North American warblers and other songbirds. From a natural history perspective, it is difficult to overstate the insights GPS technology has given us for these difficult to study species.

(d) *Conservation impacts*

In a similar vein, we argue that it has been the most basic information from GPS collars, such as where animals move, and not the fine-scale technological advances in understanding mechanisms of movements, that have so far made the most substantial contributions to conservation. In 1993, an Argos-collared wolf from the Canadian Rockies travelled over a 100 000 km^2 area in Alberta, British Columbia, Montana, Idaho and Washington, giving inspiration to the Yellowstone to Yukon Conservation initiative (Chester 2006). GPS data from pronghorn antelope in Wyoming highlighted movement corridors that were threatened by oil and gas development in a narrow migratory pinch-point (Berger 2004). What is striking about these examples is the extremely simplistic, yet convincing way in which GPS data were presented to great conservation relevance with little or no statistical analysis. This has been our experience time and time again. For example, day and night GPS maps of wolf (*Canis lupus*) telemetry locations clearly showed a dramatic avoidance of human activity—from a Park Managers viewpoint, no additional or sophisticated analysis (such as by Hebblewhite & Merrill 2008) was necessary to initiate management actions to reduce human activity. The visual appeal of GPS data speaks to its power to inform conservation with the most basic graphics and analytical metrics, and we think that this will continue to be one of the most valuable role of GPS telemetry in conservation.

(e) *Projecting impacts of climate change*

Knowledge of animal movements from GPS technology will also enable researchers to understand mechanisms of climate impacts on populations. Perhaps the most compelling conservation example that harnesses the full power of GPS technology is a recent study of the effects of climate change on the predicted distribution of polar bears (*Ursus maritimus*) in the next 50 years (Durner *et al.* 2009). Satellite-borne GPS and Argos collars have revolutionized the study of the mechanisms of climate impacts on polar bears by enabling year-round observation, revealing the circumpolar nature of polar bear movements, and the details of how sea ice depth and structure influence polar bear hunting success on their main prey, seals. Durner *et al.* (2009) combined resource selection functions built on GPS and Argos locations of polar bears from across the circumpolar arctic with biogeoclimatic models of polar ice dynamics under a variety of global climate model predictions. Based on the mechanistic links between polar bear hunting success for their main prey, seals, and sea ice thickness and structure, models predicted a 68 per cent decline in polar bear habitat in summer and 17 per cent decline in winter habitat for polar bears. Climate change will affect the distribution of seasonal forage for many other species, for example through changes in plant phenology (Post & Inouye 2008; Post *et al.* 2008) for migratory ungulates such as caribou, Mongolian gazelles and pronghorn. Therefore, we think that this GPS-born knowledge will provide ecologists with powerful tools to assess potential impacts of climate change on migration.

5. CONCEPTUAL CHALLENGES

(a) *The link between resource selection and movement*

One of the greatest challenges facing analysis of GPS data is reconciling the relationship between movement and resource selection (Turchin 1998). Since the inception of movement ecology (Skellam 1951), ecologists have tried to understand how movement drives resource selection, and vice versa, using either a Lagrangian (bottom-up from individual movements) or Eulerian (top-down from resultant distributional patterns) approach. For more details of these two approaches, see Smouse *et al.* (2010) and Turchin (1998). Numerous recent studies have demonstrated differences between resource selection and movements (Fortin *et al.* 2005; Anderson *et al.* 2008; Haydon *et al.* 2008). In a series of elegant papers, Paul Moorcroft and colleagues (Moorcroft *et al.* 2006; Barnett & Moorcroft 2008; Moorcroft & Barnett 2008) developed a Eulerian approach based on movement modelled as a diffusion process linked to the underlying ecological processes of resource acquisition and social interaction. Using a coyote dataset, they theoretically demonstrate that movement is related to the square of the resource selection function; i.e. that movement accentuates resource selection in a predictable way. Connecting movement to resource selection will allow ecologists to transcend the limitations of one particular currency of analyses in habitat ecology (i.e. time in telemetry, speed/space in movement studies), and link consequences of resource selection (see next section) to their movement mechanisms. To us, this has been among the most important recent contributions to movement ecology and will require much of the next decade to understand its significance across systems.

Ironically, these results were made possible not with the advent of GPS data, but with VHF data collected painstakingly in the field in Yellowstone National Park (again) on coyotes. Coyote telemetry data were methodically combined with spatial data on small mammal abundance (forage resources) and behaviour—scent marking—to develop a biologically realistic diffusion model that successfully predicted changes in behaviour with the removal of coyote territories in an interacting socially dynamic coyote population. The lesson here for applications of similar methods to GPS data is that careful biological measurements of resource availability and behaviour will continue to be required to complement GPS technology.

(b) *The problem of identifying biological behaviour, or the 'move'*

An important problem for which we lack a general solution is that of matching the temporal scale of data collection to animal behaviour. This is the problem that Turchin (1998) called correctly identifying the 'move'—that is, the biologically relevant movement behaviour of an animal, and not merely the discretized sampling of that 'move' by a fixed sampling interval. A growing number of statistical approaches allow us to disentangle statistical signatures in movement data that correspond to slow and fast movements, which we could interpret to be resting and moving, for example. However, we do not yet know the best temporal 'scale' to sample different species to ensure inferences from such statistical approaches match with 'real' behaviours. A few studies examine the scale-dependence of movement rates and other movement metrics from animal relocation data for certain species (Musiani *et al.* 1998; Pepin *et al.* 2004). Despite these insights, what are needed are meta-analyses across species and sampling intensities from very short (5-min) to daily fix-intervals to be able to determine the scale-dependence of movement behaviour revealed by GPS data. Furthermore, meta-analyses of the allometry of movement across a wide range of body size of taxa would allow ecologists to make *a priori* predictions about appropriate sampling strategies to be able to best identify the 'biological move'. Hopefully, cross-taxa and system meta-analyses of movement data from GPS telemetry will be facilitated through online shared databases such as Movebank (http://www.movebank.org/ see also Urbano *et al.* 2010).

(c) *The final link from movements to populations*

For GPS data to really make the link between movements and population consequences of movement, more studies need to explicitly quantify the fitness implications of movements. In this recommendation, we are in good company, for critical reviews of the field of habitat selection have come to the same conclusion (Garshelis 2000; Hirzel & Le Lay 2008; Gaillard *et al.* 2010). While numerous recent studies have made advances in movement ecology using GPS technology, ecologists would benefit by more frequently trying to connect movement and resource selection to its population consequences. There are few examples of GPS data being used to link to fitness consequences. Haydon *et al.* (2008) showed that wide-ranging movements of reintroduced GPS-collared elk were correlated with increased risk of mortality, a key link between movement and fitness. Also with elk, Hebblewhite *et al.* (2008) found that migratory elk had exposure to higher forage quality, which translated to higher pregnancy rates and calf weight. Similar examples could examine relationships between fitness components such as body size, litter size, longevity, etc., which would allow making the link between movements and fitness. Few studies have made strong links between population consequences and movements, perhaps symptomatic of a focus on the methodological aspects of GPS technology. Judicious use of GPS devices in the existing long-term studies such as the wolves of Isle Royale or Yellowstone, wildebeest and lions (*Panthera leo*) of the Serengeti, or the well-studied Soay sheep (*Ovis aries*) on St Kilda, for example, will help ecologists link movements from GPS data to fitness.

6. CONCLUSIONS: A CAUSE FOR CAUTIOUS OPTIMISM

In conclusion, we know the Craigheads would be envious of the growing insights from GPS technology (J. Craighead 1999, personal communication), and agree that the advantages of GPS technology may outweigh costs for certain ecological and conservation questions (table 1). However, ecologists have a number of important issues to recognize when conducting GPS-based studies of animals. First, there are substantial risks in terms of compromising good study design principles, risks to animals during repeated captures, overestimating the general importance of fine-scale data to ecology and the real risk of continuing to divorce biologists from the field where insights to animal ecology must always come from. We highlighted several examples of what we consider misuse of GPS technology for the wrong reasons. The meretricious allure of increasingly sophisticated approaches to the analysis of GPS data needs to be tempered with a firm foundation in ecological processes for the real power of GPS technology to be borne. We think that an important area in which researchers could improve GPS technology is to collect finer spatial and temporal scale information about the resources and behaviours that were present at the actual GPS location of the animal. This could be achieved through combination with advances in remote sensing (e.g. MODIS or hyperspectral imagery), animal-borne sensors (e.g. cameras, Moll *et al.* 2007), contact collars for social interactions, (Handcock *et al.* 2009) or plain old fieldwork facilitated by real-time GPS location uploading (e.g. fieldwork following animals tracks on the ground—kill sites, vegetation sampling, etc.). Only by combining the real power of GPS data with the kind of field biology that made the Craighead's leaders in animal ecology and conservation can ecologists really hope to make the kinds of advances that we claim GPS technology will bring us.

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