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How Tracking Technology is Transforming Animal Ecology: Epistemic Values, Interdisciplinarity, and Technology-Driven Scientific Change

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Abstract

Tracking technology has been heralded as transformative for animal ecology. In this paper I examine what changes are taking place, showing how current animal movement research is a field ripe for philosophical investigation. I focus first on how the devices alter the limitations and biases of traditional field observation, making observation of animal movement and behaviour possible in more detail, for more varied species, and under a broader variety of conditions, as well as restricting the influence of human presence and observer bias. I reconstruct these as shifts in scope, objectivity, accuracy and fruitfulness. The second transformation is slightly less obvious but equally significant for animal ecology. Tracking devices generate complex data that demands both statistical and biological expertise, which has led to increasingly frequent and intensive collaborations between statisticians and biologists. Based on interviews, I examine how researchers in these interdisciplinary collaborations negotiate the collection, analysis and interpretation of movement data, integrating research interests, methodological constraints, previous field observations, and background theory. Tracking technology is therefore also shifting which disciplinary considerations are brought to bear on research into animal movement and behaviour and how this research is conducted.

Keywords: Movement ecology; Biotelemetry; Data-centric science; Interdisciplinarity; Scientific change; Objectivity; Fruitfulness

1 Transformations in Animal Ecology

Behavioural biologists and ecologists are excited about animal tracking technology. Using GPS trackers, radio tags, accelerometers, and other devices, biologists can observe animals' locations as well as behavioural phenomena such as foraging, predation, or migration. The devices enable observations of large numbers of individuals with little human interference, for many different species, over vast distances, and even underwater or in dense foliage. Movement data can be analysed alone or combined with ecological and physiological data to investigate causes and consequences of animal behaviour (Dodge et al. 2013; Williams et al. 2020). Tracking technology can also improve conservation, for instance by indicating locations, seasons or times of day in need of protection (Katzner and Arlettaz 2020; Ogburn et al. 2017).

In line with broader movements towards data-centric biology (Leonelli 2016), tracking technology is transforming animal ecology and the knowledge it generates. Researchers in the field frequently celebrate the new possibilities that tracking technology offers, as exemplified in a recent review paper:

> Recent technological advances in data collection and management have transformed our understanding of animal "movement ecology" (the integrated study of organismal movement), creating a big-data discipline that benefits from rapid, cost-effective generation of large amounts of data on movements of animals in the wild. These high-throughput wildlife tracking systems now allow more thorough investigation of variation among individuals and species across space and time, the nature of biological interactions, and behavioral responses to the environment. (Nathan et al. 2022)

This enthusiastic vision of data-intensive animal ecology is echoed by other researchers in the field. Tracking technology has "smashed" traditional limits on behavioural observation (Brown et al. 2013, p. 1), offers "paradigm-changing opportunities" (Williams et al. 2020, p. 187), and has "revolutionized research in animal ecology" (Börger et al. 2020, p. 6). Whenever biologists get talking about tracking devices there is a palpable air of excitement at their transformative potential, as I have witnessed in many presentations and meetings.

Philosophers of science are yet to explore this rapidly evolving field and its surrounding fervour. In this paper I begin to address this lacuna. By examining how tracking technology is transforming animal ecology, I make a case for animal movement ecology and its associated technological transformations as a field ripe for philosophical investigation. As a case study, I draw on the work of a number of biologists and statisticians studying the movements of pinnipeds—flipper-footed marine mammals such as seals and walruses.[1] I conducted semi-structured interviews with four researchers, as well as attending a number of talks and having informal discussions over several years. To complement this small case study, I incorporate insights from methodological and review literature.

[1] To protect the identity of the researchers, the species names are not disclosed.

I focus first on the transformations most discussed by biologists. Tracking devices enable the observation of animal behaviour in more detail, for more diverse species, and under a greater variety of conditions, all with less time spent on painstaking field observations and less influence from human observers (Brown et al. 2013; Nathan et al. 2008; Williams et al. 2020). Tracking technology thereby reduces biases and limitations present in traditional field observations and provides more detailed information about animal movement and behaviour. I reconstruct these changes in terms of shifts with respect to several key epistemic values: scope, objectivity, accuracy, and fruitfulness. This reconstruction builds on philosophical literature about the role of epistemic or cognitive values in scientific change (e.g., Douglas 2013; Kuhn 1977). Whereas most literature has focused on how epistemic values, such as simplicity, scope, fruitfulness, or coherence, are used to evaluate and select theories, I show how similar epistemic values are also important in the evaluation and adoption of new scientific technology. Animal movement ecology therefore offer a new context for philosophers to explore the role of epistemic values in contemporary research.

Second, I argue that tracking technology is transforming how decisions are made about collecting, processing, analysing and interpreting movement data. Animal ecology has long drawn on theoretical elements from other disciplines, especially economics models and evolutionary theories (Bolduc 2012; Grüne-Yanoff 2016; Stuhrmann 2022). Tracking technology has led to new sorts of interdisciplinarity emerging for animal ecologists, leading them to engage with new disciplines and in more intensive collaborations. Specifically, decisions about animal tracking data take place in intensive interdisciplinary collaborations between biologists and statisticians, involving the iterative integration of research interests, methodological constraints, previous field observations, and background theory from each field. Such interdisciplinary collaborations are crucial for deriving meaning from big, complex tracking data. By looking closely at these collaborations, we gain a better understanding of the transformations taking place in animal ecology: as well as changes with respect to epistemic values, tracking technology is also broadening the disciplinary considerations brought to bear on the study of animal movement and behaviour and how this research is conducted.

Movement ecology therefore mirrors similar shifts towards inter- and transdisciplinarity in genomics, systems biology, and other data-centric disciplines in biology and biomedicine (MacLeod and Nersessian 2013; Richardson and Stevens 2015). More generally, the changes taking place in movement ecology support the argument that understanding scientific change requires attention to scientific collaborations and the conditions under which these collaborations take place (Andersen 2016; Ankeny and Leonelli 2016; Canali 2022). As in previous studies of interdisciplinary collaborations, studying collaborations in movement ecology reveals iterative processes of integration, alignment and interlocking (Andersen and Wagenknecht 2013; MacLeod and Nersessian 2016). Attending to collaborations in movement ecology thereby complements other studies showing that data-centric research involves not merely an increase in the amount and speed of data collection and analysis, but also significant transformations in scientific practices and communities (Callebaut 2012; Canali 2016; Gross et al. 2019; Krohs 2012; Leonelli 2016; Ratti 2015).

I begin in Section 2 by introducing tracking technology and describing how it is used to study animal movement and behaviour. In Sections 3 and 4 I consider how tracking devices affect scope, objectivity, accuracy, and fruitfulness. This is followed by Sections 5 and 6, where I investigate the interdisciplinary collaborations between biologists and statisticians. I conclude in Section 7 by summarising how tracking technology is transforming science and where this might take philosophers of science. Many other actors are of course involved in these changes to animal ecology, from individual non-human animals to the military-industrial complex (Benson 2010). Nevertheless, tracking technology is the transformative agent I focus on in this paper.

2 Technology for Tracking Animals

The use of electronic devices to track animals is known as biologging, animal telemetry or biotelemetry. In this section I introduce biotelemetry, providing the groundwork for later investigating the changes it is inducing in animal ecology.

Since the 1950s, biologists have been tracking animals with very high frequency (VHF) radio transmitters, and more recently with satellite-based systems such as Argos and global positioning system (GPS) devices, acoustic and light signalling systems, accelerometers, and other technologies (Benson 2010). General technological developments over the past 30 years have greatly contributed to animal tracking being more affordable and feasible for various research contexts (Benson 2010, 2016; Nathan et al. 2008; Williams et al. 2020). These developments include satellite and mobile technology, smaller and more powerful batteries, tiny solar panels, 3D-printing for waterproof cases, greater data storage and transmission capacities, and so on. The result is affordable, accurate and relatively small tracking devices, with companies offering off-the-shelf trackers for research as well as domestic purposes. As one of my interviewees recounted, tracking collars for pet cats can be cheap alternatives to purpose-built tracking devices. Movement tracking devices are often combined with environmental and physiological sensors, and sometimes with audio-visual capacity, enhancing the breadth of information gathered (Williams et al. 2020). Devices can either transmit or archive data; archival tags must be retrieved by researchers to download the data, but they save on battery life and thus longevity or size.

Responding to these technological advances, biotelemetry grew in popularity throughout the 2000s, resulting in a number of high-profile reviews (Nathan et al. 2008; Rutz and Hays 2009; Schick et al. 2008). 2013 saw the founding of two journals, *Animal Biotelemetry* and *Movement Ecology*, the latter including all taxa but in practice focusing largely on animals. By the early 2020s, movement ecology is an established field with dedicated journals, methods, scholarly societies, research groups, and textbooks (Demšar et al. 2015; Edelhoff et al. 2016; Hooten et al. 2017; Nathan et al. 2008). In addition, biotelemetry is becoming a well-established technique across behavioural ecology, functional ecology, community ecology, population ecology, behavioural biology and conservation biology (Williams et al. 2020).

Tracking technology delivers information about animals' location and movements, relevant for studying phenomena such as species distribution, migration routes, or the location and timing of foraging (Demšar et al. 2015; Nathan et al. 2008; Schick et al. 2008). It can also be used to study behaviour, such as foraging behaviour or conspecific interactions, by using complex statistical models such as hidden Markov models to infer behavioural states from movement data (Börger et al. 2020; Hooten et al. 2017; Schick et al. 2008; Williams et al. 2020).[2] Movement ecologists often summarise their questions about animal movement and behaviour with lists of four questions. For instance, Nathan et al. (2008, p. 19053) list the questions: "(i) why move? (ii) how to move? (iii) when and where to move? and (iv) what are the ecological and evolutionary consequences of movement?" Williams et al. (2020) consider a similar set of four questions: (i) where is the animal going? (ii) how is the animal moving? (iii) what is the animal doing? and (iv) why is the animal moving? Another set of four questions is listed by Hooten et al. (2017, Chapter 1), where animal telemetry helps answer fundamental ecological questions about animals' (i) space use, (ii) movement, (iii) resource selection, and (iv) behaviour.

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[2] Hidden Markov models are used to infer the behavioural states that underly observed movement data (Langrock et al. 2012). Researchers classify behavioural states according to patterns in the step length (distance travelled between observations) and turning angle (change in direction between observations). For instance, a long step length and minimal turning angle is classified as travelling since it indicates that the animal is moving across large distances without changing direction; in contrast, a small step length and high turning angle may be classified as foraging or searching a small area.

These four-part lists include both *descriptive* and *explanatory* goals. On the one hand, biologists aim to describe where animals are located, when and where they move, how they are behaving, and what resources they use. This is a key goal since surprisingly little is known about the habitats, migration, behaviour, social interactions, and resource use of many species in the wild (Brown et al. 2013). It is also important for conservation, for instance in determining when and where fishing should be restricted to avoid conflicts with foraging animals or in identifying where wind turbines should be placed to minimise collisions for soaring birds of prey (Börger et al. 2020; Katzner and Arlettaz 2020; Ogburn et al. 2017).

On the other hand, researchers aim to study mechanisms, causes and consequences of animal movement. For instance, researchers identify environmental or ecological causes by looking at how animal movement is correlated with abiotic factors, interspecific interactions or intraspecific (social) relations (Dodge et al. 2013; Nathan et al. 2008). Biologists also look at how an animal's internal state, such as neurology, physiology, or energy use, affects or is affected by movement (Owen-Smith et al. 2010; Williams et al. 2020). Finally, researchers study the effects of movement on fitness, niches, or population dynamics (Spiegel et al. 2017; Williams et al. 2020). The study of multiple causes and consequences promises to enhance the understanding of animal movement and can also help predict the impact of habitat loss and climate change (Hebblewhite and Haydon 2010; Ogburn et al. 2017; Schick et al. 2008).

Whether it is used for descriptive or explanatory projects, tracking technology is transforming how biologists study animal location, movement, and behaviour. Some of these transformations are practical and economic. For instance, biotelemetry can alleviate costs for large numbers of field workers trained in behavioural observation or time spent observing behaviour (Hebblewhite and Haydon 2010; Hooten et al. 2017). However, biotelemetry doesn't eliminate fieldwork. Scientists must attach devices to animals, monitor equipment, retrieve archival tags for data download, take VHF recordings using portable radio receivers, and perform many other tasks associated with collecting high quality tracking data. One interviewee, for instance, explained how they had to check whether animals were still alive to verify that recorded movement was of a live animal and not a corpse being moved by scavengers. Tracking devices are also still fairly expensive, and researchers have to trade-off cost with technical capacities and ethical requirements. As one interviewee recounted,

> For all animals there are very strict ethical requirements for the size and weight of the GPS tag. And the more frequently you record a GPS location, the larger the battery needs to be, and the larger battery, the heavier the GPS tag. So you kind of have to find this in-between balance between size and weight of the tag and length of the battery life. And cost, so you can get really small and light tags that have a very long battery life, some of them even have solar panels on them. But for every

> tag you'll pay hundreds upon hundreds of dollars or euros. Our tags, because we wanted to buy 100 of them, we couldn't spend that much money. So our tags cost 60 dollars [each].

Thus, although biotelemetry research promises economic and practical advantages, it still involves considerable labour, equipment, and time costs.

Aside from economic and practical changes, biotelemetry's major transformations concern the knowledge about animal movement and behaviour it can help to generate. Biologists discuss two major epistemic transformations: a reduction in bias and an increase in detail compared to traditional field observation. In the next two sections, I reconstruct these transformations as a shift with respect to four major epistemic values: scope, objectivity, accuracy, and fruitfulness. This reconstruction connects biologists' discussions to broader philosophical discussions about scientific change, showing how technologies, not just theories, are evaluated and adopted in light of epistemic values. It also helps to highlight the epistemic risks and limitations of tracking technology and its widespread adoption. Overall, the reconstruction helps to support animal movement ecology as an area worthy of future investigation by philosophers of science interested in scientific change and values in science and provides material for a more in depth examination of many of the epistemic values I survey here.

3 Overcoming Observational Limitations and Biases

Tracking technology is widely praised in movement ecology for the way it helps to overcome limitations and biases affecting behavioural observation. Traditional field observations are restricted to what a human can witness. To get a sense for just how challenging this can be, consider this introduction to a recent special issue on biologging:

> Imagine yourself, as an ecologist during field work, deep in the woods. *Eerily silent was the forest, when loudly from the tree above a wren started to sing. A quick, skilful use of the binoculars showed it was the male ringed last week, but swiftly the bird disappeared again among the leaves.* Similar difficulties in reliably observing the behaviour of the study species will be familiar to many ecologists and can strongly affect the choice of the study species. (Börger et al. 2020, p. 6, emphasis in original)

Foliage, topography, rain and storms, as well as turbidity and depth of water, all obstruct direct vision and can limit auditory monitoring. Many animals have natural tendencies to avoid humans, although some can be habituated to human presence (Brown et al. 2013). Animals may spend significant amounts of time hidden in burrows, hollows, or similar structures. With camouflage and mimicry, animals can blend into the background or be indistinguishable from other species. The large distances covered by migratory animals make it difficult for researchers to keep up observations over the entire migratory route. Many animals are active primarily or exclusively at night. Finally, there are many animals in remote locations inaccessible to research teams.

These challenges place distinct limitations on behavioural observation in the field and generate several sorts of bias. Researchers study only a select number of readily observable species and focus on directly observable behaviours (Börger et al. 2020). In addition, human presence can alter animals' behaviour or the behaviour of non-focal species such as predators or prey. This means behavioural and ecological knowledge is not necessarily representative of the great diversity of species or even the behaviour and ecology of a single species (Brown et al. 2013). In addition, there are observational biases due to what humans tend to notice or find interesting, which are minimised but not eliminated by the use of ethograms and inter-coder reliability tests (Brown et al. 2013; Burghardt et al. 2012; Marsh and Hanlon 2004; Tuyttens et al. 2014).

Biologging devices circumvent many of these limitations. As a number of researchers have echoed, tracking technology is seen as a tool to "observe the unobservable" (Brown et al. 2013; Williams et al. 2020, p. 187). One interviewee explained the importance of their tracking data on pinniped's diving behaviour:

> Without the dive data we would have actually no idea where they [the animals] are really going. Because we cannot read flipper tags when they are in the water, and we cannot see how deep they're diving otherwise. So without the dive computers we would get nothing there.

Similarly, another interviewee used tracking devices to observe the movement of pinniped pups under dense foliage and amongst large groups of mothers and pups.

Tracking devices thus enable the study of more diverse species under a range of conditions and absent the immediate influence of human presence, removing many sources of bias (Brown et al. 2013; Cooke et al. 2013; Demšar et al. 2015; Hebblewhite and Haydon 2010; Hooten et al. 2017). As Hebblewhite and Haydon (2010, p. 2308) state, "From a natural history perspective, it is difficult to overstate the insights GPS technology has given us for these difficult to study species." These changes can be reconstructed as shifts with respect to two key epistemic values: scope and objectivity.

First, tracking technology broadens knowledge about animal movement and behaviour to cover more diverse species und different conditions. This increases the *scope* of animal ecology, that is, the extent to which its claims apply to more of the living world (Douglas 2013). Biologists value scope insofar as it means they have more knowledge about more parts of the living world, but also because it can aid conservation efforts for more species and ecosystems in response to threats such as climate change and habitat loss. They also value broader scope because it can help them to develop more general theories of animal movement within and across phyla, guilds, niches, habitat types or ecosystems.

Second, and partly as a consequence of the previous point, biotelemetry affects the *objectivity* of research on animal movement and behaviour. Objectivity is a complex concept with a complex history (Daston and Galison 2007; Douglas 2004). Rather than delving into the philosophical discussions about the nature of objectivity, I focus on distinguishing how tracking technology affects different sorts of objectivity, with the aim to understand the changes taking place in animal ecology.

One sort of objectivity commonly valued in the sciences is *procedural objectivity*. Procedural objectivity is generally characterised as the exclusion or elimination of researchers' idiosyncrasies, preferences, or individual judgements in data collection, analysis, interpretation or communication, so that different researchers can use the same procedure and obtain the same results (Douglas 2004; Jukola 2015). Tracking technology, for instance, enhances procedural objectivity by reducing the idiosyncratic effects of observer bias. This improvement in procedural objectivity is one reason why biologists value such technology.

Yet, as biologists are fully aware, tracking technology doesn't eliminate all idiosyncrasies and individual judgements from the research process. There are many sorts of decisions to be made about data collection, processing, and analysis (see Sections 5-6). For instance, one biologist I interviewed reflected on how their decisions about how to analyse their tracking data influenced the number of behavioural states included in the resulting model:

> It's still subjective. Because in the end it's me behind there looking which states make the most sense. Because you can see what fits best, but sometimes you have like oh here a three and four state both makes sense—but what makes biologically most sense? And yeah it would be really cool to find a way to make it more objective because in the end you could look at it and say, yeah, this is the only logical conclusion in the end, but… still, there are certain decisions I had to do. To say okay this here is a traveling state, or here it makes only sense to look at a two state approach.

As this biologist describes and as movement ecologists generally recognise, tracking technology does not eradicate the influence of individual judgements and perspectives. But biotelemetry does enhance procedural objectivity in some respects and to a certain degree.

In addition to removing some idiosyncratic observer biases, tracking technology also helps to overcome more general biases faced by all researchers employing traditional observational techniques, such as the choice of study species and observational conditions or the influence of human presence. One of the major sorts of objectivity at stake here is what we could call *taxonomic objectivity*: the reduction of the impact of idiosyncratic or community-wide factors that bias choice of study species.

Recent discussions in ecology, evolutionary biology and conservation biology have brought up the problem of *taxonomic bias*, or *taxonomic chauvinism* (Bonnet et al. 2002; Troudet et al. 2017). In these fields, some taxa such as birds are over-represented and others such as insects under-represented in publications and publicly available datasets. Taxonomic bias can be caused by societal values such as preferences for charismatic or endangered species affecting funding sources or data provision (Troudet et al. 2017), personal preferences of reviewers and editors for species they are more familiar with (Bonnet et al. 2002), and a lack of suitable or readily applicable methods for understudied species, which in turn results from the lack of investment in method development for these species (Pawar 2003). Many of these factors are common criteria for choosing which organisms to study (Dietrich et al. 2020). Such criteria, applied judiciously, may serve experimental biologists well in picking out a suitable model for a phenomenon of interest. However, when the goal is to study particular and heterogenous natural systems in their full diversity, as is frequently the case in ecology, evolutionary biology and conservation biology, choices about and restrictions on which species are studied can strongly bias the resulting knowledge of biological diversity.

By facilitating the study of more varied species, tracking devices can address some of the sources of taxonomic bias. In the process, they enable researchers to gain knowledge that is more likely to be representative of both general trends and naturally occurring diversity in movement and related phenomena. In other words, biotelemetry can enhance taxonomic objectivity. On the other hand, tracking devices also have their own taxonomic biases: some species resist attempts to be harnessed with a tag (Potvin 2022; Semmens et al. 2007), others may be too small to carry a tag or move in environments where tags are too obstructive, and there are ethical restrictions on tagging certain species (Benson 2010). Tracking technology therefore enhances but does not maximise taxonomic objectivity.

Biotelemetry may also involve shifts in other sorts of objectivity. As I discuss in Sections 5 and 6, effective use of tracking devices often requires interdisciplinary collaborations. This means that more diverse perspectives are brought into the study of animal movement and behaviour. Diversity is in turn supportive of *interactive* or *strong objectivity*: roughly speaking, a social understanding of objectivity as something requiring open discussion and mutual criticism amongst members of a diverse scientific community (Douglas 2004; Harding 2015). Diversity can support interactive objectivity in that more diverse participants are better able to critically evaluate common assumptions or methodologies or contribute new knowledge and research questions overlooked by more homogenous communities (Harding 2015; Longino 1990). Interdisciplinary collaborations in movement ecology may similarly enhance interactive objectivity. In collaborations, statisticians and biologists explain and justify their decisions, critically evaluate unfounded assumptions or inappropriate uses of devices and statistical methodologies, and contribute statistical and biological knowledge in an explicit and justified way (see Sections 5 and 6).

Discussions about tracking technology can easily fall into tropes of scientific technology transcending human perceptual limitations and providing a view from nowhere. Such narratives have been criticised for overlooking both the continued importance of human perspectives in the construction and use of measurement instrumentation, and the ways technology itself can direct the course of scientific research (Boon 2015; Daston and Galison 2007; Haraway 1988). Biologists' rhetoric does sometimes tend to portray tracking technology as inducing a great improvement in scope and objectivity and nothing else. Nevertheless, in their more reflective moments biologists clearly recognise the complexities of the changes taking place in their discipline. In a critical review, two biologists warned of the dangers of an increasingly remote animal ecology:

> 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. (Hebblewhite and Haydon 2010, p. 2306)

This lack of field experience, they argue, can limit the ability to assess the representativeness or biological importance of biotelemetry studies. As I discuss in Sections 5 and 6, researchers do in fact recognise that experiences from the field and biological expertise continue to be crucial for collecting, processing, and analysing tracking data. Nevertheless, care is needed in ensuring that such local knowledge continues to be appreciated as important for the study of animal movement and behaviour, rather than being eliminated or sidelined in favour of technological solutions.

4 A Data Rich Discipline

As well as overcoming observational limitations and biases, tracking devices are celebrated for their ability to generate large amounts of data. Movement ecology is a data-centric or "data rich discipline" (Demšar et al. 2015; Nathan et al. 2022). GPS trackers, for instance, can record values every five minutes or even more frequently (though every hour is more common due to constraints on battery size), and accelerometers commonly record multiple readings per second. Such fine-scaled measurements of animal location and movement in the wild over weeks or months are genuinely novel, exceeding human observational abilities (Demšar et al. 2015; Hebblewhite and Haydon 2010).

Biologists value the new insights such high-resolution and long-term data can provide. For instance, one interviewee talked about how GPS devices enable them to look at each pup's movement track for around two months after birth.

> For the pups we wanted to look at their movement in more detail. [We attached very small GPS tags] right at birth and then we left the tags on until they started molting. The GPS loggers recorded a GPS position for every pup every hour. And then we could download this data at the end of the season and then we had a really nice track of where the pups were throughout this early life stage.

Another interviewee stressed how surprised they were by how much information about animal behaviour they could get from tracking devices.

> I would have never guessed that we would be able to get in so much depth with the dive computers, with the biologging devices. [...] I have such great resolution, where I really can distinguish where they [the animals] are foraging. So now I don't have just GPS plots everywhere they go, but really can see they are foraging here.

The excitement about the volume of data that tracking data provides is related to two epistemic values: accuracy, and fruitfulness.

First, increasing the frequency of observations and thereby the resolution of tracking data can reveal movements and behavioural patterns not captured by more coarse-grained data. For instance, higher-resolution data can reveal that fish avoid fishing vessels using fine-scaled movements, or reveal overlooked conspecific interactions that are significant for avian-borne disease transmission (Nathan et al. 2022). Tracking technology can therefore help to produce a picture of animal location, movement and behaviour that is closer to where, when and how animals are actually moving, with less distortion and abstraction. In other words, biotelemetry is more *accurate*. Philosophers discussing epistemic values and scientific change typically focus on theories, and they consequently define accuracy as a match between theory, on the one hand, and data or empirical evidence, on the other (Douglas 2013; Kuhn 1977; Longino 1996). The accuracy delivered by tracking technology is different: it concerns the fit between data or models, on the one hand, and some aspect of the phenomenon of interest, on the other (Bokulich and Parker 2021; Weisberg 2006). In other words, tracking technology improves not the fit between theory and data, but rather the fit between data (or data models) and the world. Movement ecologists value increased accuracy in this second sense: as discussed in Section 2, knowing where, when and how animals are moving is a central goal in movement ecology, and this goal can be better achieved by increasing accuracy.

Although it is more accurate, higher-resolution data is also typically more complex and difficult to analyse. In addition, some level of detail is unnecessary. Five-minute GPS recordings, for instance, may not reveal any more important details than hourly recordings, depending on the species and behaviour of interest. Accelerometer data is in fact often too detailed, requiring down-sampling prior to analysis. More generally, fine-scaled movements may not always affect the phenomena which researchers aim to describe or explain (Hebblewhite and Haydon 2010). Researchers therefore aim to generate data that is fine-grained enough to accurately capture the movement or behaviour of interest, but not so fine-grained that it contains unnecessary detail or redundant data points. In other words, movement ecologists prioritise accuracy with respect to the phenomenon of interest, but they also recognise other epistemic values such as simplicity, tractability or explanatory power as reasons to avoid unnecessary detail.

As well as increasing accuracy, the large amount of data generated by tracking technology allows researchers to investigate new and understudied phenomena, such as individual differences, developmental and seasonal changes, long distance migration, and a variety of other movement-related phenomena (Börger et al. 2020; Nathan et al. 2008, 2022; Spiegel et al. 2017). Tracking technology is therefore *fruitful*: it helps to reveal new phenomena and produce new scientific findings. Fruitfulness is often attributed to scientific representations, such as theories, hypotheses, or models (Douglas 2013; Elliott and McKaughan 2014). For instance, Thomas Kuhn presents fruitfulness as an important criterion of theory choice, arguing that "a theory should be fruitful of new research findings: it should, that is, disclose new phenomena or previously unnoted relationships among those already known." (Kuhn 1977, p. 75) Philosophers of science have more recently argued that instruments, technologies and methods also play important epistemic roles in science, including revealing new phenomena and opening up new research directions (reviewed in Boon 2015). Biotelemetry provides a good example of the way technological improvements can be fruitful, bringing to light new phenomena and thereby contributing to scientific change.

For example, tracking devices can be used to follow a large number of identifiable individuals continuously for extended periods of time. Such large amounts of individual-level data are truly novel. Although traditional methods such as bird ringing or capture-recapture methods can provide individual-specific data, the datapoints are limited to resighting or recapture events and are thus sparse over time and space. Similarly, newer technology such as camera traps provide lots of data, but for many species we have no reliable methods for individual reidentification. Tracking technology thus provides an unprecedented capacity to study movement and behaviour at the individual level.

Biotelemetry has become an important tool in the broader shift in behavioural ecology and related disciplines towards studying individual differences and using individual-based approaches (Justus 2014; Sarkar 2016; Weisberg 2014; Wilson 2004). Having multiple observations for a single individual is essential for studying phenomena such as animal personality and individual ecological specialisation, because these phenomena generally require an individual to be consistent over time (Trappes 2022; Trappes et al. in prep.). In addition, tracking relatively large numbers of individuals is important for comparing individuals' behaviour to measure between-individual variation. Tracking technology can therefore be used to identify individual differences in traits such as exploratory tendency, foraging style or habitat preference in the field and with minimal human intervention, and even investigate possible causes and consequences of individual variation (Nathan et al. 2022; Spiegel et al. 2017).

Tracking devices also greatly enhance researchers' ability to study long distance movements of animals such as migration. Although techniques such as bird ringing, birdwatching, or whale watching do deliver findings about migration timing and major routes, they do not typically allow researchers to follow in detail exactly how, when and where migratory animals travel. Tracking technology, by providing detailed, long-term observations of animal's movements, have revealed startling insights about distances travelled and routes taken by migratory and even non-migratory animals (e.g., Houstin et al. 2022; Lai et al. 2022). In addition to simply enhancing the ability to observe travelling animals, tracking devices also produce data that can be readily correlated with meteorological, environmental and other sources of data. This allows researchers to identify and investigate patterns in migration timing and routes and how they are affected by weather events, environmental changes, and human disturbances in a way that would not be possible without such fine-grained data (Nathan et al. 2022).

Tracking technology is fruitful, but it also introduces distinct limitations on what sorts of behaviour can be studied. Not all behaviours can be easily inferred from location and movement data (Buderman et al. 2021). For instance, spatial proximity between two animals can result from a social interaction of many different sorts (prosocial, aggressive, competitive, cooperative, copulatory, etc.), and it could even be that the animals are unaware of or ignoring each other. Biotelemetry therefore cannot easily be used to distinguish and investigate distinct conspecific interactions, limiting the sorts of questions biologists can ask about social behaviour.

Tracking technology also tends to facilitate the study of spatiotemporal location over behaviour. Interpreting the behavioural meaning of statistical patterns in movement data requires information gathered from field observation, previous studies, and background theory (see Section 6). Even when this sort of knowledge about local context and expected behaviour is available, often very complex models are needed to analyse tracking data to study behaviour. Given these complexities, researchers might prioritise the relatively straightforward use of tracking data to investigate spatiotemporal location. Again, this can place limitations on what phenomena are studied by movement ecologists.

Biologists therefore ought to be careful about the consequences of a wholesale adoption of tracking technology, given the ways this will shape the directions future research will take. It may be that the phenomena that tracking technology provides access to are the ones that biologists see as most important to study. Knowing migration routes, for instance, is likely more useful for developing conservation policies than knowing precise details about mating dynamics. Similarly, recording spatiotemporal location such as species distribution is often instrumental for instituting conservation policies such as protected areas. In other words, the value of fruitfulness may be inflected by other values and goals, including broader societal concerns such as conservation.

Feminist philosophers have in fact critiqued fruitfulness as placing value in studying any new phenomenon without distinguishing which phenomena are most important to study (Longino 1996). Movement ecologists do seem to prioritise certain new phenomena rather than celebrating any new phenomenon that technology can be used to study. However, more attention is needed to which research directions are being prioritised through the growing use of tracking technology: why are certain phenomena seen as important, and is this appropriate? For instance, tracking technology may favour broad-scale conservation approaches, such as instituting conservation areas, over more local efforts focused on breeding or foraging behaviour. Evaluating the way tracking technology is shaping animal ecology therefore requires reflection on non-epistemic values and goals.[3]

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[3] Interestingly, Helen Longino (1996) argues that attention to individual differences falls under a feminist theoretical virtue (specifically, ontological heterogeneity). There may therefore be feminist reasons to value tracking technology and its usefulness for studying individual differences, apart from novelty. This connection is an intriguing topic for future research.

To sum up, tracking technology's epistemic transformations of animal ecology relate to its ability to overcome limitations and biases of traditional field observation. Biotelemetry enables the study of a broader range of species and conditions while limiting human presence and observer biases, as well as providing a more detailed picture of animal movement and facilitating the identification and investigation of new phenomena and patterns. Reconstructing these benefits in terms of epistemic values helps to recognise that biologists prize biotelemetry not simply for the volume of data it delivers, but rather for its consequences for scope, objectivity, accuracy and fruitfulness. It also highlights how transformations in movement ecology are shaped by different weightings of epistemic and non-epistemic values, such as prioritising accuracy over simplicity or prioritising conservation policy development over understanding animal behaviour. Finally, it helps to identify some of the limitations of tracking technology, especially with respect to objectivity and fruitfulness, and the consequent risks involved in its widespread adoption. Of necessity, this reconstruction of the role of epistemic values in movement ecology has remained relatively superficial. Future work is therefore needed to expand this survey by exploring particular values both in more depth and in light of broader discussions on values in science and scientific change.

5 Interdisciplinarity in Movement Ecology

Tracking technology is transforming our knowledge of animal movement and behaviour. However, actually attaining this knowledge requires more than simply attaching devices to animals. Biotelemetry data is highly complex and must be carefully collected, processed, modelled, and interpreted to derive useful information about animal movement. This process often relies on interdisciplinary or multidisciplinary collaborations between biologists and statisticians, mathematicians, computer scientists, geographers, and physicists (Williams et al. 2020). In this and the next section I discuss how researchers negotiate these interdisciplinary collaborations, focusing on collaborations between biologists and statisticians. Statisticians have led the charge in developing models for analysing movement data, and have written textbooks and methods papers for movement ecology (Hooten et al. 2017). They are also often involved in project-specific collaborations with biologists, advising about study design and data collection, and performing data processing and analysis, model refinement and communication in publications. Examining these collaborations reveals how tracking technology is transforming the disciplinary perspectives brought to bear on animal ecology.

Collaborations between statisticians and biologists in biotelemetry research sometimes begin prior to data collection. Statisticians can advise biologists on what data to collect, how frequently to collect it, how it should be structured, and so on. The aim at this stage is to make sure the data obtained suits the needs of the modelling techniques and can ultimately answer the biologists' research questions. For instance, one interviewee, a biologist, recounted their discussions with statisticians during data collection.

> When I came back from my first field season, I sat down with [the statisticians] and we looked at the data. They kind of had a preliminary look at how the data looked, how well it was structured, how much data we were missing. And they gave us feedback on what would be helpful for them. So, for example, we decided that the movement looked a bit jerky recorded at one GPS recording every hour. So we agreed in the next field season to do a trial run for a shorter period of time for a few individuals where we recorded GPS at a higher frequency. […] And this would then allow them to verify that the data that we had collected at one hour intervals was actually representative of what was actually happening. […] And then we spent a lot of time discussing the different external and internal factors that we wanted to include in our model. […] Then we talked a lot about how the data needed to be structured. Then when I came back from my second field season we had this additional data and I knew exactly how to merge all of the files with all of the different categories that we were looking at and how they needed the data structured to feed it into what they were building.

Collaborating at the data collection stage avoids problems with data that make analysis difficult or impossible.

In particular, there are considerations from statisticians that may not have occurred to biologists, such as getting a temporal resolution that is neither too coarse nor too fine, or having regular recording intervals rather than pausing recording when animals are expected to be inactive. Early discussions can thus avoid the disappointment of being unable to analyse carefully collected data. As one statistician recounted,

> When I talk to a biologist, it's really, I mean most of the time they are really enthusiastic, which is great and then they have all these great huge datasets. That's also really, really cool. But when you look at what you can do with it, there are limits. So very often I mean you have to discuss and then decide OK, unfortunately, we just cannot include that into the model.

To avoid these awkward situations, statisticians prefer to guide biologists on which data to collect. Already at the data collection stage, then, researchers shape what gets observed based on what can be effectively modelled to answer particular research questions. This is in addition to the constraints on data collection due to practical, economic and ethical considerations.

More frequently, collaboration with statisticians first starts after data collection. One interviewee, a statistician, described the process of working with biologists on animal movement data.

> Before we fit the first models, we would already have spent […] at least a couple of hours discussing the research objective, the data, problems with the data. […] there would be this iterative process that I start with a simple model, we go back and discuss things, then I start trying out slightly more complex models, more refined models to capture more patterns, to make more of the data. […] there would be 3, 4, 5 iterations every time involving me reporting what I've found and then the ecologists trying to make sense of it with me together. Actually, we will discuss this together, usually. And at some point we would probably settle on a model formulation. I would then do all my model checks and prepare graphics and everything, and then the whole interpretation again would be fairly interdisciplinary. I mean, we would discuss things first of all together, then the biologists would probably write the interpretation of the results, but I would then help with making sure that everything is sound statistically. So it's actually very intensive, these collaborations.

As this quote highlights, interdisciplinary collaboration covers data processing, multiple iterations of model development, as well as interpretation and paper writing. Both statisticians and biologists provide inputs and engage in dialogue at each of these steps.

Importantly, the collaboration involves iterations of repeated consultations and independent work. As Williams et al. (2020, p. 188) put it, biotelemetry "operates via collaboration between disciplines in a system of feedback loops." This iterative structure has also been observed in other interdisciplinary settings. For instance, systems biologists solve complex and unstructured modelling problems through iterative adjustments in concepts, methods, data, and the problems themselves, a process that is also ideally aided by repeated interactions with experimental biologists to test and acquire data for the models (MacLeod and Nersessian 2013, 2016). Iterative processes of interaction and adjustment have also been recognised as theoretically important for achieving strong integration between contributions from different disciplinary backgrounds in interdisciplinary contexts (Andersen and Wagenknecht 2013).

Iterative collaboration enables researchers to gradually deal with a major challenge inherent in interdisciplinary research: how to combine perspectives, methods, concepts, standards, theories, technologies, and so on from different disciplines into a single research project or field (Andersen and Wagenknecht 2013; MacLeod 2018; MacLeod and Nersessian 2013). Philosophers of science have pointed to the need for *exchange*, *alignment* or *interlocking* in interdisciplinary collaboration, which are extended processes in which participants communicate their own assumptions and disciplinary backgrounds, learn about or acquire some aspects of other disciplines, and build up a shared scientific repertoire (Andersen 2016; Ankeny and Leonelli 2016; Canali 2022; Grüne-Yanoff 2016; MacLeod 2018). In the next section I examine how biologists and ecologists in movement ecology perform these sorts of activities when processing, analysing and interpreting animal tracking data.

6 Integrating Perspectives on Movement Data

When dealing with animal tracking data once it has been collected, biologists and statisticians contribute their expertise in a series of decisions about data processing, modelling and interpretation. The models and interpretations of animal location, movement and behaviour that result are the joint outcomes of an integrative process that involves a heavy burden of communication and mutual learning.

Some biologists downplay their role in model development and interpretation, viewing statisticians as the primary authors of the model and construing their own role as limited to data collection and writing up papers. However, statisticians stress the importance of the biologists' input about the research objectives, data, species under study, and so on. One statistician recalled that a major challenge in the early days of animal movement ecology was the expectation that they could analyse data without concrete research questions.

> First challenge: ecologists who collect animal movement data without a specific research question and then come to me and say you have all these fancy modeling techniques, give me something which I can publish. And I say well, what do you want to find out? They say, I don't know but I have these cool data.

As the interviewee went on to explain, there is now greater awareness of what sorts of research questions can be answered with movement data and more targeted collection and use of movement data. In addition, the development of standard analytic tools and modelling procedures through question-driven research was needed to make data-driven approaches more feasible in movement ecology (Williams et al. 2020).

As well as the research questions to ask, data processing relies crucially on biological information. For instance, one interviewee recounted a problem they had in their dataset, where the tracking devices had occasionally recorded zeros instead of "NA" for missing values. This created highly unrealistic movement patterns. Dealing with this problem meant deciding how far an animal could possibly travel and using this as a threshold for a realistic movement pattern. This decision was made in collaboration between the biologist and the statisticians, based on preliminary data and the biologists' field observations of animal movement.

The importance of integration is even more apparent when it comes to model development. One statistician discussed how making and justifying assumptions in the model is difficult without contact with the biologists.

> The more input I get from the biologist, the easier it is for me to formulate a model, to make assumptions and also to explain them, to justify them. Because I mean when you write about them, you need to have your reasons.

For example, in developing hidden Markov models a choice must be made about how many and which behavioural modes to include in the model. This decision depends not just on how the model fits the data, but also on what other evidence is available and whether it makes sense from a biological perspective (Brown et al. 2013; Hooten et al. 2017; Williams et al. 2020).

Another interviewee, a biologist, recounted the discussions they had with a statistician about their models. Initially, it seemed a three-state model worked best, identifying how the animals travel to foraging areas, search an area for food, and then forage. However, for a certain subset of the data, it seemed that the three-state model did not fit. After much debate and analysis, they decided that the population contained a group of individuals that had only two behavioural states, travelling and foraging. The biologist explained that searching wasn't necessary for these animals because they fed not on mobile fish shoals but rather from the sea floor, something that could be identified by looking at the location data and the resources present at different locations. The biologist highlighted the importance of their own contribution to movement data analysis.

> I think because it always needs to be analyzed from a biological perspective, it would have not been possible just to give [the statistician] the data and say please do some hidden Markov models. It was really the cooperation. I would not have been able to do it on my own. Not at all. But this quite close cooperation between the two of us, I think, managed to get those really exciting [findings].

As this interviewee stresses, successful model development in movement ecology requires a biological perspective, such as knowledge about the target species' behaviour and environment. A similar view was voiced by a statistician.

> It's all just data driven, so of course as long as we don't have additional information or additional observations really telling us that yes, the animal at that moment is really foraging, we actually can't know. It's just how we interpret it. It might be very likely because we see this and that. But yeah, still…

Field observations and background theory, then, are crucial to construct models and support inferences from the model's states to animal behaviour. These must be integrated with statisticians' techniques, methods, and standards in the iterative process of interdisciplinary model development.

Statisticians thus rely heavily on biologists for their expertise, and through collaborations they learn about and adapt to biologists' research questions, theoretical perspectives, and background knowledge. Similarly, biologists have to learn about sophisticated statistical methods and how to correctly interpret models. One biologist emphasised how much they learnt from their collaboration with statisticians.

> I was never trained in statistics or in mathematics, and they were. So it was really nice to kind of see their perspective on how to analyze data. […] a lot of their perspectives and insights are relevant not only for this paper, but also for all of the other data sets that I analyze, so I think it was really, really helpful.

One approach in particular involved deciding which additional explanatory variables to include in a model. The biologist had recorded environmental conditions, physiological parameters, and morphological features, variables they chose based on earlier studies, theories about animal behaviour, and field observations. They then worked with a statistician to apply sequential model adjustment to determine which parameters are explanatory and which could be left out of the model. The biologist appreciated the approach because it allowed them to explore all the biological variables they had hypothesised to be relevant, rather than cherry-picking based on statistical significance.

The mutual learning between statisticians and biologists can be seen as an instance of *interlocking*, the acquisition of a basic version of the elements of another research domain through interdisciplinary collaboration (Andersen 2016). Interlocking is important to facilitate communication across disciplines, which is often a serious challenge in interdisciplinary research due to differing and often opaque assumptions and standards (MacLeod 2018; MacLeod and Nersessian 2013). However, even with interlocking there are limitations in how much each member of a collaboration can understand and evaluate with respect to other disciplines (Andersen 2016). For instance, one statistician described their difficulties in communicating with biologists to ensure they correctly interpret a jointly developed model.

> Of course the more complex the model, the more difficult to make sure that everyone else understands what you're doing. I had some problems actually with making sure that a biologist understands that we just assume something. Because he always said like, well, that's the result, where the result is that there's an interval of three hours in which they are less active. But actually that was an assumption made within the model.

The interviewee went on the explain that one of the major tasks of a statistician is communicating analyses and results in a way that is understandable to people without statistical expertise, including their biologist collaborators. Similarly, statisticians are also often involved in writing up published papers, to ensure that models are interpreted correctly and that important limitations are discussed.

Both biological and statistical expertise are important for collecting, processing, and analysing movement data. These two forms of expertise could be embodied in one person.

However, seeing them separated in interdisciplinary collaborations makes the contribution of each and the process of their integration especially apparent. The disciplinary separation helps to highlight the way research questions, assumptions, background theories, field observations, and the demands of statistical methods thoroughly shape the collection, processing, modelling and interpretation of animal tracking data. It also highlights the iterative process of interlocking and alignment, including mutual learning, adjustments, and incorporation of disparate elements. One of the transformations brought about by tracking technology is therefore a shift in who is involved in studying animal movement and which disciplinary considerations are brought to bear on and integrated in choices about data and models.

7 Conclusion

Tracking technology is transforming animal ecology. Biologists are excited about these transformations and often present a very enthusiastic vision of the new data-centric movement ecology. In this paper I have examined the transformations being wrought by tracking technology with an eye to epistemic values as well as the growth in interdisciplinary collaborations. As I have shown, movement ecology is highly relevant to a number of important debates in philosophy of science and is a promising field for future exploration.

By enabling the study of a wider variety of species under more varied conditions, over sustained time periods and in greater detail, biotelemetry overcomes limitations and biases inherent in traditional field observation, provides a more accurate picture of animal movement and behaviour, and enables access to new and understudied phenomena. Biologists value the changes in scope, objectivity, accuracy, and fruitfulness that tracking devices enable, partly for epistemic reasons of improved knowledge of the living world and partly for the role this knowledge can play in conservation. However, reflection is needed on how biologists evaluate tracking technology and its limitations and risks. In particular, I highlighted how individual judgements, taxonomic limitations, and local knowledge continue to play a role in biotelemetry tracking technology, as well as how biologging privileges certain sorts of research topics in a way that is inflected by broader scientific and social values and goals. Further work is also needed to explore each of the epistemic values I considered in more detail to better account for how they are understood in animal ecology as well in statistics and other disciplines with which animal ecologists collaborate, how tracking technology may be shaping this understanding, and whether alternative understandings could be more appropriate.

Biotelemetry also involves frequent interdisciplinary collaborations between biologists and statisticians, from the data collection stage through to data processing, analysis and interpretation. Due to the differences in expertise and disciplinary perspectives, each party to the collaboration can more readily notice and describe their own role and the role of the other party. This highlights how research interests, methodological demands, assumptions, background theories, and field observations all feed into data collection and processing, model development, and interpretation. Tracking technology thereby transforms who is doing research in animal ecology, what disciplinary considerations are brought to bear on this research, and how the research is done, adding iterative processes of alignment between biologists and statisticians, including mutual learning, adjustment, and incorporation of disparate elements. This interdisciplinarity also makes more transparent to biologists how their own research interests, background theory and field observations matter to the process of collecting, analysing and interpreting biotelemetry data, even though this data is collected remotely rather than with their own senses.

More and more ecologists are working at their desks rather than in the field, partly due to the growth of technology like tracking devices and remote sensors that collect and transmit big data. Time will tell how this affects the kinds of considerations that go into studying animal movement, when researchers may not have their own field observations or hands-on experience with animals, their environments, and the technology to draw on in making decisions about data and models. But a fully remote movement ecology is at any rate a distant possibility. At present, employing tracking technology and processing, analysing and interpreting the data still requires field researchers with expertise in dealing with animals, ensuring the technology is functioning, gathering data, identifying potential failures or sources of error, and observing animals in the field. And this biological expertise must still be integrated with statistical expertise to produce descriptive and explanatory knowledge about animal movement and behaviour. It is this interdisciplinary practice as well as the enhancements in scope, objectivity, accuracy, and fruitfulness that tracking technology brings to animal ecology.

This study of the transformations taking place in animal ecology opens up a number of future research directions beyond those already embarked upon in this paper. First, although I considered interdisciplinarity and epistemic values largely separately in this paper, it would be interesting to explore how different values are prioritised in different disciplines and whether and how these differences are negotiated in the iterative processes of collaboration.[4] Second, the generation of large quantities of standardisable quantitative data, together with the growing trend to make this data publicly available on online databases, greatly enables data reuse in synthesis studies and meta-analyses of animal behaviour (Kays et al. 2021). This raises questions about how field experiences and background knowledge might feed into data reuse, how standardisation will affect the sorts of research questions being explored, and what the role of synthesis studies is in contemporary ecology (Trappes under review). In addition, the ability to integrate ecological and meteorological sensors in tracking devices is leading to an increased use of animals as mobile environmental sensor devices (Max Planck Society 2021). This promises to widen the disciplines interested in tracking animals and the sorts of questions that can be asked and answered, as well as raising questions about the employment of animals as observational agents (Benson 2010, 2016). Finally, biotelemetry devices are selective in the sorts of behaviour they can capture, and this behaviour must be operationalised in terms of signals in movement or acceleration data. Tracking technology may therefore have consequences for which behavioural phenomena are frequently studied and may even affect how behaviour is conceptualised in animal ecology. All in all, movement ecology is a promising field for philosophers of science interested in the changing nature of contemporary life sciences.

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