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PERPECTIVES AND PARADIGMS

Tracking invasive animals with electronic tags to assess risks and develop management strategies

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Abstract Invasive species alter ecosystem structure and function when they establish in new habitats. Although preventing or managing invasions is extremely important for maintaining biodiversity, doing so is difficult and requires efficient intervention. Remote monitoring of free-living animals with electronic tags (i.e. tags that transmit data remotely or log them for future retrieval) can contribute important knowledge about invasive animal biology. A quantitative literature review identified instances in which electronic tagging has contributed to studying invasions. Electronic tags were generally used for one of four purposes: (1) characterize spatial ecology; (2) identify interactions; (3) assess risk potential; or (4) evaluate management options. Overall, electronic tags have considerable potential for developing, refining, and evaluating invasion management strategies that contribute to conservation efforts. We explore the role of electronic tags as a component of integrated control program design and implementation for invasive animals.

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Introduction

Monitoring individual animals is fundamental to the study of natural history, ecology, animal behaviour, and physiological ecology (Cooke et al. 2004; Patterson et al. 2008; Spicer and Gaston 2009). Observations provide information about physiological processes, individuals, populations, and communities that are necessary for effective management and conservation. Time and space constrain the ability of biologists to make direct observations on animals, but the development of electronic tagging tools (i.e. biotelemetry and biologging devices) has provided a method for remote monitoring of free-living animals (Cooke et al. 2004; Rutz and Hays 2009). Electronic tags can be attached or implanted to provide information about an animal's behaviour and physiology by logging information for later retrieval or by transmitting information to a receiver (including satellites) that communicates with the tag. These electronic tags have generated ecological information that is not easy to obtain via direct observation and have provided insight into animal ecology that has been useful for a variety of basic and applied research and management programs (e.g., Cooke 2008; Hussey et al. 2015; Wilmers et al. 2015; Wilson et al. 2015). Despite these advances, it is unclear to what extent electronic tagging is used in the study of biological invasions, an ecological problem that is considered a major contributor to the global biodiversity crisis (Gurevitch and Padilla 2004).

Invasive animals are those that have been introduced beyond their native range and successfully survive, reproduce, spread, and may have negative impacts on native communities where they have established (Box 1). The establishment of an invasive species in an ecosystem can lead to the erosion of ecological linkages among species by introducing new competition for resources or inciting antagonistic interactions such as predation or parasitism between invasive and native animals. Information about the behaviour (Holway and Suarez 1999) and the physiology (Lennox et al. 2015) of invasive species is important for understanding their interactions within novel environments. For example, introduced animals must rapidly adapt to locally available sources of food and shelter and to locally abundant predators while maintaining contact with a small number of conspecifics for reproduction to establish as invasive species (Henry et al. 2013). These challenges require behavioural acclimatization and the ability to do so indicates the likelihood that an animal will become invasive. Additionally, invasion success is a function of physiological acclimatization, or the ability to perform under local climatic conditions (e.g., Braby and Somero 2006). The behavioural and physiological data that are useful for answering the fundamental questions about animal invasions can be obtained from free-living animals using electronic tags. Such information is especially useful for developing and implementing management strategies that aim to assess the consequences of invasive animals at various stages of an invasion (see Blackburn et al. 2011), as well as to predict, prevent, and control biological invasions.

Managing biological invasions calls for an integrated approach based on scientific evidence about the biology of the invasive species. Electronic tags represent a valuable tool for studying invasions and developing interventions by enabling rapid and accurate assessments of free-living animals. Indeed, electronic tagging can provide information about the behaviour and physiology of animals to document movement patterns and habitat preferences, and model interactions between invasive and native species in a new range. Resulting data can contribute to predictions about whether the species will become invasive and to the testing of potential control protocols before implementation.

Whether non-native species pose risks to local ecosystems is a prominent conservation concern because of the damaging impacts these species have when they become invasive. However, invasions are a multi-stage process and conservation efforts can suffer when monitoring individuals is difficult, particularly early on when intervention is most important. Given the rapid expansion of electronic tagging technology and its applicability for many conservation problems (Cooke 2008), we wondered whether and how electronic tags are being used for addressing this conservation problem. In this review, we evaluate the role that electronic tagging plays in invasive animal species research to determine the extent to which electronic tagging is integrated within such research, and to identify opportunities for further integration as biological invasions continue to represent a prevalent conservation issue.

Approach

Relevant literature for a quantitative review was identified in Thomson's Web of Science database (Thomson Scientific 2014). Web of Science was selected because it is comprehensive, has inter-search repeatability, allows the incorporation of Boolean operators within the search phrase, provides filters to remove spurious hits, and gives the option to download results for quantitative analysis. However, Web of Science searches have limited searching power because the engine searches only article *topics* for search terms (i.e. title, abstract, keywords, keywords plus; Thomson Scientific 2014). Therefore, the Web of Science is useful to assess trends using quantitative analysis, but does not provide exhaustive lists of literature for a comprehensive literature review. To add to our review, we therefore performed auxiliary searches using Google Scholar to identify the maximum number of potentially relevant articles related to invasive species and telemetry. Whereas results from the auxiliary search are incorporated throughout the manuscript, data for the quantitative analysis and corresponding figures are restricted to the Web of Science results to ensure repeatability.

Web of Science was searched for quantitative review materials on March 31 2014 for articles containing words in the topic indicating research was being conducted on invasive animals (invas* and/or "non-native" and/or alien and/or "non-indigenous" and/or "foreign species"). Additionally, topic words indicating that the study involved the use of electronic tags (telem* and/or biotelem* and/or tag* and/or *logg* and/or track* and/or GPS (global positioning system) and/or "global positioning" and/or transmitt* and/or transpond* and/or radio and/or VHF and/or "very high frequency" and/or acoustic and/or ultrasonic and/or PIT) were queried (Table 1; see also Cooke et al. 2013). The results from Web of Science were refined to include results only up to the end of the year 2013 and only from the following disciplines: ecology, marine/freshwater biology, fisheries, zoology, biodiversity conservation, and environmental sciences. All resulting articles were considered after reading the title and abstract, and articles that were not relevant to our search were excluded. The final list of relevant articles was downloaded for quantitative analysis.

Finally, we categorized articles based on the study objective for a qualitative review of the relevance of electronic tagging in invasive animal research. The four categories that we identified for the qualitative review were: evaluating spatial ecology of invasive species, studying interactions between native and non-native species, assessing invasion risks posed by non-native species, and testing preventive or control mechanisms for managing invasive species (Box 1). The qualitative review expands on the findings from the Web of Science search by incorporating additional studies that were not identified in the quantitative review, but that fit into the four categories that we identified.

Findings

Quantitative literature review

Our search of the Web of Science yielded 96 peer-reviewed research articles that implemented electronic tags to study free-living invasive animals, often in the wild but also in controlled settings such as mesocosms. The search identified articles beginning in 1999, with increasing instances of integration of electronic tags in invasive animal research since then. It is possible that the search failed to detect papers for which electronic tags were used to study an invasive species if it was not explicitly noted as an invasive species in the title, abstract, or keywords. Similarly, some studies use electronic tagging to study invasive species in their home range (i.e. where they are not invasive) simply to

Table 1 Several electronic tags can be used to study invasive animal behaviour and physiology

Electronic tag	Data collection limited by	Data download	Dominant habitat	Key benefits	Primary function	Example
Acoustic transmitter	Design of receiver array	From acoustic hydrophone receivers	Aquatic	Accurate 3D positioning in water	Positioning aquatic animals	Zimmermann et al. (2013)
Biologger	Retrieval of loggers	Directly from the logger	Aquatic/ terrestrial/ aerial	Collect physiological data	Collecting physiological or behavioural data	Hays et al. (2007)
GPS collar or pop-up satellite tag	Battery life	From satellites	Aquatic/ terrestrial/ aerial	Tracking large-scale movements	Positioning animals	Spencer et al. (2012)
Passive integrated transponder (PIT)	Number of PIT logging stations	From a fixed logging station	Aquatic/ terrestrial	Inexpensive	Monitoring movement past a gate	Bravener and McLaughlin (2013)
Radio transmitter	Number of logging stations/ frequency of manual tracking	Collected actively with a receiver or downloaded from a fixed receiver station	Aquatic/ terrestrial/ aerial	Actively tracking animals	Positioning animals	Kobayashi et al. (2006)

understand their spatial ecology; it is unlikely that such studies would have been identified in our search although we submit that they are outside the scope of this review. In 2013, 18 studies were identified, the highest annual publication output representing 19 % of all studies identified (Fig. 1).

Among the 96 studies identified, radio telemetry was the most common method, likely due to its versatility for tracking free-living aquatic, terrestrial, and aerial animals (Fig. 2). Only three studies incorporated biologging technology. The 96 studies monitored the impacts of a variety of invasive animals, most commonly invasive mammals, fishes (Class Osteichthyes), and crayfishes (Class Malacostraca; Fig. 3). The resulting studies were categorized into four research objectives (summarized below in the Qualitative Literature Review); 92 of the 96 studies were effectively categorized, however four studies were categorized as “other.” Research objectives of these four studies that could not be categorized with our scheme were developing tagging methods on invasive species or monitoring fine-scale behaviour or physiology from a fundamental perspective. Many (51 %) of the studies identified by our search focused on characterizing the spatial ecology of invasive animals, for instance using electronic tags to calculate home range or identify habitat preferences. Other studies used electronic tags to identify interactions between invasive and native animals, generate predictions or risk assessments about the invasiveness of an animal, or evaluate management-oriented hypotheses about invasive animal control (Table 2).

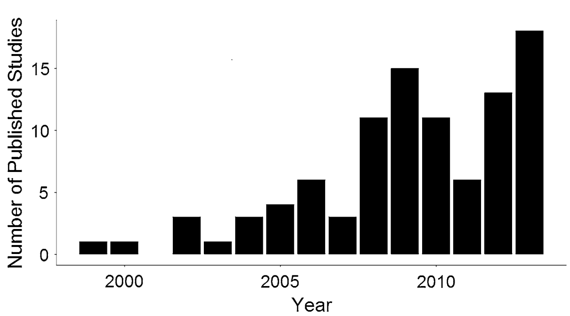

Fig. 1 Distribution of published studies incorporating telemetry for studying invasive species by year. The first instance identified in a review of Thomson Scientific’s Web of Science was in 1999 with the highest annual publication output occurring in 2013

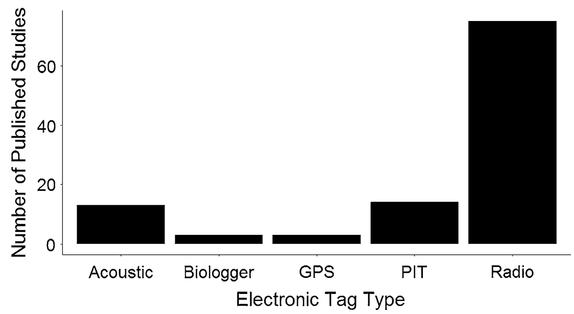

Fig. 2 Electronic tag types used for studying invasive species based on a review of Thomson Scientific’s Web of Science. The figure shows a breakdown of which electronic tags are more commonly used to study invasive species. Studies that used multiple tag types are represented multiple times. See Table 1 for tag type details

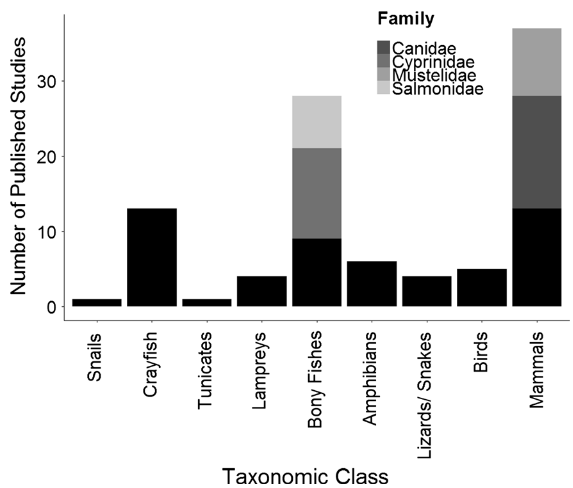

Fig. 3 Distribution of focal taxa in published literature concerning both invasive species and telemetry. Thomson Scientific’s Web of Science search engine was used to identify 96 relevant papers and focal taxa were categorized based on taxonomic class. Common names corresponding to taxonomic classes are included to demonstrate the focal subjects of studies. Some taxonomic families are also included for illustration. If studies featured multiple invasive species, the study is represented multiple times

Qualitative literature review

Characterization of the spatial ecology of invasive species

Tracking invasive animals and their relationship with their new environment provides important information about their ecology. In addition to providing

Table 2 Solutions that incorporate electronic tagging are offered to a suite of common problems associated with biological invasions. Management interventions are either measuring the consequences of, predicting, preventing, or controlling an invasive species

Problem	Management intervention	Solution offered by electronic tagging
Will a species (should it be introduced into the local habitat) become invasive?	Predicting or preventing an invasion	Simulated invasion by releasing tagged individuals into an enclosure or into the environment; monitor habitat selection, interactions with native species, and survival (e.g., Dorcas et al. 2011; Zimmermann et al. 2013)
Can a non-native species successfully reproduce and become invasive?	Predicting or preventing an invasion	Tag and track a potentially invasive species to identify whether it nests (e.g., Pernas et al. 2012) or participates in reproductive aggregations
How can the spread of invasive species be contained or controlled?	Preventing or controlling an invasion	Tracking data from established invasive species can be used to identify dispersal tendencies or calculate the home range of the species. Such data can be used to identify locations where traps or barriers will have success and times of day or seasons during which trapping initiatives can be most effective
How will an invasive species affect the local native biota in similar niches?	Assessing the impacts of an invasion	Tracking invasive species, native species, or both in combination can provide information about their interactions. Tracking can elucidate whether invasive species will take over an existing niche or whether there can be coexistence (e.g., Medina-Vogel et al. 2013; Wiens et al. 2014)
Is there appropriate forage for a potentially invasive species in a new range?	Predicting an invasion, Assessing the impacts of an invasion	Monitoring the diet of a non-native species can help determine whether the local available food will allow the species to become invasive; this can be achieved by tagging native species and/or the invasive and tracking behaviour. Tracking invasive species can also lead to identification of latrines, scat, or carcasses that can be used to identify dietary constituents (e.g., Jiménez et al. 2013)
Can culling, barriers, or traps be effective for managing a biological invasion?	Controlling an invasion	Tagging and tracking the behaviour of an invasive species relative to a barrier or trap can help managers quantify the effectiveness of the intervention (e.g., Reinhardt et al. 2009). Tracking representatives of a gregarious species (the 'Judas' technique) can also allow managers to identify aggregations or cryptic individuals for culling or management (e.g., Parkes et al. 2010)

fundamental information about the invasive species, tracking animals reveals the way in which they interact with their environment and this knowledge can be instructive for management of the species. Indeed, eradication of invasive species is ideal to eliminate their negative impacts on local environments (Clout and Veitch 2002), but setting traps or establishing barriers that reduce the population size of an invasive species can also be useful for limiting the spread and localizing the impacts of the invasive species when eradication is impossible or impractical. Determining how invasive animals use habitat in their new range is important for developing trapping protocols or implementing barriers, especially knowing where and when animals move across the landscape. Before initiating control measures, monitoring the way invasive animals interact with the environment is important for providing information necessary for successfully implementing such strategies.

Movements may occur constantly when animals are nomadic, daily within a home range, or seasonally based on migratory trajectories. Spencer et al. (2012) used GPS tags in an attempt to identify patterns in space use or aggregations of tagged dromedary camels (*Camelus dromedarius*), which are invasive in Australia, but found that control would be logistically impossible due to their unpredictable wandering and lack of aggregation. Many invasive animals are not nomadic, though, and may establish more predictable movement patterns that are distinct across ontogenic, spatial, or temporal trajectories. Snapping turtles (*Chelydra serpentina*) are invasive in Japan and are long-lived and late-maturing, meaning that effective control efforts focus on adult removal. Kobayashi et al. (2006) radio-tagged snapping turtles and found that although juveniles were found in agricultural areas, the large turtles remained in the rivers where they could be targeted for removal. Seasonally, or at different life history stages, invasive animals may increase activity (Ringler et al. 2014), initiate dispersal, or migrate, which can be monitored with electronic tags. Sea lamprey (*Petromyzon marinus*) is a migratory agnathan fish that is invasive within the Laurentian Great Lakes. Migratory corridors, aggregation points, and activity periods have been determined from electronic tagging (Holbrook et al. 2014). Sea lamprey demonstrate how patterns in behaviour can be life-stage specific or may change seasonally, meaning that seasonal changes in movement or habitat use can be exploited for management. Some species may even form spawning aggregations. Gregarious behaviour or aggregations can be targeted by managers via the 'Judas' technique, in which some representatives from a population are electronically tagged and tracked as they move into an aggregation, leading managers towards a large number of individuals that can be trapped or culled together (Taylor and Katahira 1988). Bajer et al. (2011) found that common carp (*Cyprinus carpio*) exhibit gregarious behaviour in winter, and that tagging and tracking some representatives of the population contributed to more efficient removal of the species from a lake. Using electronic tags to study the movement and habitat use of invasive species is an important step in understanding the invasion, indeed, movement provides context for other phases of an invasion including which native species will interact with the invasive species and determining whether adjacent habitats are at risk of further invasions. Studying movement of invasive species also provides critical information to management and control.

Identification of interactions between invasive and native species

When a non-native animal species is introduced to a new range, it will have to integrate within the native community to survive. Ensuing interactions between the invasive animal and native community will be entirely novel to the invasive species. Species that become invasive will establish and cause disruption to the native community by antagonizing native species (via predation, parasitism, or intoxication), competing against native species, or hybridizing with native species (Gurevitch and Padilla 2004). Theoretical models of invasion biology may be inaccurate for predicting whether invasive species can coexist with native species via resource partitioning or whether an invasion will result in competitive exclusion and local extinction of native species (e.g., Bolger and Case 1992), making field observations, which can be facilitated by electronic tagging, especially important.

Interaction between native and non-native species is an important process in invasions. Species that become invasive must often become successful competitors of native species or else be excluded from resources and become extinct in the invaded range. Identifying associations between native and invasive species as well as behavioural changes resulting from niche infringement by invasive species can contribute towards quantifying the effects of invasions for native competitors, which can be enabled by electronically tagging invasive and/or native species. In some cases, native species can adapt to the presence of invasive species and they can coexist via resource partitioning (e.g., Medina-Vogel et al. 2013). In other instances, however, competition can be damaging to native populations. Wiens et al. (2014) used electronic tags to identify changes in movement, habitat selection, and reproductive output of native Northern spotted owls (*Strix occidentalis caurina*) as a result of increasing interactions with encroaching barred owls (*Strix varia*).

Electronic tags can also be used to identify the fate of native species in the presence of invasive species to calculate perceived and actual risks associated with invasions. Recio et al. (2013) monitored habitat use of GPS-tagged European hedgehogs (*Erinaceus europaeus*) to determine whether they were likely to interact with nesting shorebirds; however, predation by hedgehogs was deemed unlikely because hedgehogs avoided the floodplains, a finding that could save unnecessary trapping efforts in riparian zones. Hybridization between competing native and invasive species can worsen the negative impacts of biological invasions. Muhlfeld et al. (2009) tracked spawning locations of native west slope cutthroat trout (*Oncorhynchus clarkii lewisi*) and invasive rainbow trout (*O. mykiss*) and identified considerable risk of hybridization and reduced genetic integrity. Fish that escape from aquaculture operations often pose a threat to local native populations if they rejoin native stocks. With acoustic telemetry, Zimmermann et al. (2013) found that emigration of farmed Atlantic cod (*Gadus morhua*) after simulated escape from aquaculture was rapid and that the farmed individuals joined native stocks. When farmed fish intersperse with native stocks, there is high potential for hybridization, which results in outbreeding depression via introgression of maladaptive genes into the population. Thorstad et al. (1998) evaluated the potential for escaped farmed Atlantic salmon (*Salmo salar*) to enter coastal spawning rivers and determined, from radio telemetry data, that farmed salmon in River Namsen, Norway were distributed in similar locations as native salmon during the spawning period, indicating a high probability of hybridization and introgression of domesticated genes.

Assessment of risk for potential invasion

Proactive measures to prevent biological invasions are often the most effective method of invasive species management, because established invasive species can be very difficult to eradicate (Ricciardi and Rasmussen 1998; Leung et al. 2002). Knowing which species pose invasion risks can make invasive species management more effective by identifying species that pose actual, as opposed to perceived, risks to local ecosystems. The ability to predict invasions before they occur and identify real threats represents an important research objective that can contribute to preventive measures against the establishment or survival of invasive species by spurring appropriate action against an invasion before it occurs (Kolar and Lodge 2001). To identify real invasion threats, factors that contribute to the establishment of an invasive species must be considered; these can include abiotic and biotic factors such as behaviour and physiology.

For a non-native species that becomes invasive, the novel range must provide favourable biotic and abiotic habitat features to support the species. Determining which habitat features are necessary to invasive species is important when projecting where the invasive species may spread. Tagging and tracking established invasive animals in a new habitat can reveal habitat preferences by determining how much time individuals spend in certain habitats. When habitat preferences are identified, risk assessments can be executed to evaluate whether nearby or connected areas are at risk of invasion. Even when appropriate habitat exists, however, there may be additional factors that will affect the establishment of an invasive species, and electronic tagging can be used to test whether a potential invasive species represents a real risk by monitoring behaviour and physiology in a new habitat (Table 2). For example, Dorcas et al. (2011) monitored the movements and body temperatures of Burmese pythons (*Python bivittatus*) in a mesocosm in South Carolina. Because appropriate biotic habitat for the pythons exists in South Carolina, there was a perceived risk that the species could spread from Florida and establish as invasive; however, the tagged pythons did not survive the cold winter weather and the invasion risk could be downgraded. Although some snakes tried to adapt their behaviour to survive the cold (i.e. behavioural thermoregulation), none were successful, and some even exhibited basking behaviour in the cold indicating cognitive or behavioural impairment.

Behavioural processes are important factors when monitoring an invasion risk. Invasive species must be able to adapt their behaviour to their new range, a process that can be monitored with electronic tags. For instance, Kowalcyk and Zalewski (2011) found that invasive raccoon dogs (*Nyctereutes procyonoides*) behaviourally thermoregulate in shelters to withstand cold climates, indicating that this species can expand its invasive range beyond that which would be predicted by distribution modeling based on temperature tolerance. Changes in reproductive behaviour may result from stress or environmental differences that alter hormone cycles, changes that could potentially offset the risks of an invasion if the animal species is not able to successfully reproduce. Electronic tagging can allow monitoring of reproductive behaviour by using position data to identify reproductive aggregations. However, tagging can also be used simply to follow animals to reproductive aggregations or nests to confirm successful reproduction (e.g., Pernas et al. 2012). There are also emerging opportunities to use continuous animal positional tracks derived from electronic tags to identify behaviours such as foraging, for example by using state-space statistical modelling techniques that permit the inference of component behaviours from movement tracks of free-living animals (Patterson et al. 2008).

When external conditions for invasion are optimal, there are intrinsic characteristics of animals that contribute to their success as invasive species, and intuitively not all animals that are introduced to a new range will become invasive there (Williamson and Fitter 1996). Identifying traits shared among invasive species that may contribute to their invasiveness can allow species to be identified as an invasion risk (Kolar and Lodge 2001). Although it is difficult to predict with accuracy which species will become invasive, it is possible to generalize traits that associate with invasiveness to make predictions easier (e.g., Ehrlich 1986). As such, the identification of traits associated with invasion success has become an objective of invasive species studies (Kolar and Lodge 2001). Electronic tracking can monitor behavioural and physiological processes that contribute to invasion success. Llewelyn et al. (2010) analyzed movement speeds of invasive cane toads from radio telemetry data and found that cane toads at the range edge were more active than those at the interior of the population's distribution, indicating that locomotory plasticity is an important factor that affects invasive species spread. In addition, Henry et al. (2013) measured resting behaviour of house sparrows (*Passer domesticus*) and found that introduced individuals suffered from rest disorders that could affect the ability to become invasive. Using behavioural and physiological data to develop and test hypotheses about traits that relate to invasion success is an important opportunity provided by electronic tags.

Evaluation of management option

Once invasive animals establish, managing or controlling the invasion is necessary for minimizing their ecological impact. Managing invasions often begins only after introduction to reduce establishment or after establishment in an attempt to reduce the spread of the species, eradicate it, or maintain the population at low density (Simberloff 2009). Often, management involves the use of barriers or traps to contain an invasion, but may also incorporate more directed measures such as active trapping or culling to eradicate the invasive species.

Barriers can be erected to restrict movement. However, the effectiveness of barriers for stopping animal movement can be difficult to evaluate, because passage is not always obvious, making electronic tagging important for evaluating the effectiveness of barriers. For example, Jackson (2001) radio tagged hedgehogs to test the effectiveness of fenced enclosures for excluding the invasive species from accessing wading bird nesting sites. In many instances, however, physical barriers are not always feasible, and as such, non-physical barriers that exploit sensory physiology of animals are increasingly common to inhibit movements of invasive species, especially in aquatic environments. Noatch and Suski (2012) identified a variety of non-physical barriers for aquatic species; however, the success of different types of non-physical barriers is context-dependent because species morphology or physiology and different hydrographic regions contribute to the effectiveness of a non-physical barrier. Electricity can induce tonic immobility of aquatic species and electric barriers have been installed to prevent movement of invasive fishes from the Mississippi River drainage into the Laurentian Great Lakes. The barrier was considered an experimental application for several reasons, especially its exceptionally large size, bidirectional electric field to prevent both upstream and downstream fish passage, and given the water velocity and conductivity at the site (Sparks et al. 2010). To test the effectiveness of the apparatus for preventing fish passage, Sparks et al. (2010) tagged common carp and tracked their movements relative to the barrier and monitored their passage through it. Electronic tags represented a useful tool for calculating the effectiveness of the barrier for containing the spread of invasive species. These methods can also be applied on land to test the effectiveness of fences or barriers at preventing the passage of invasive species.

Traps can be effective for containing invasive animals that migrate or disperse when they are placed in a high traffic corridor. Passive traps require understanding the spatial ecology of animals because to be effective they must be placed in areas where they are likely to be encountered. Trap placement benefits from electronic tagging and tracking because it can determine whether traps are frequently encountered. For instance, Bravener and McLaughlin (2013) used PIT telemetry to determine that lamprey traps in the St. Mary's River, Canada were ineffective because lamprey infrequently encountered them. Subsequently, telemetry could be used to determine where traps may be placed to increase encounters. This type of information about where, when, and how to most effectively manage invasive animal species can be gathered efficiently from electronic tagging programs that identify movements, home ranges, habitat use, and activity periods.

In many terrestrial environments, barriers are impractical and invasive animals must be directly removed, rather than contained. For large-bodied or gregarious species, hunting or culling can constitute an effective means of population control. Culling can be facilitated by identifying aggregations via the tagging and monitoring of 'Judas' individuals that lead managers to conspecifics. Woolnough et al. (2006) initiated a study to evaluate the usefulness of the 'Judas' technique for European starling (*Sturnus vulgaris*) in Australia, but found it was more effective for population surveillance than for informing control efforts. However, Parkes et al. (2010) released radio-collared sterile feral pigs (*Sus scrofa*) on a Californian island to help locate pigs that had evaded previous control measures and were invulnerable to hunting and trapping. They found 'Judas' pigs to be effective, because cryptic individuals were identified and exposed by the tagged pigs. The 'Judas' technique has been appraised with electronic tags for several taxa and represents an important component of invasive species managers' toolboxes to facilitate targeting of either cryptic individuals or aggregations of individuals in an invasive population.

Only one study in our review implemented telemetry to monitor the effectiveness of biological control in managing an invasion. Comeau et al. (2012) tagged transplanted (although native) rock crabs (*Cancer irroratus*) near blue mussel (*Mytilus edulis*) farms in an attempt to control the invasive *Ciona intestinalis* tunicates that were damaging the farming equipment. Although Comeau et al. (2012) tested a native species for controlling the invasive tunicates, electronic tags could be similarly deployed for evaluating biological control in mesocosm experiments or in natural environments. Indeed, biological control can be highly effective for managing invasive species, but carries significant risk if the control agent affects non-target species, disperses out of the control area, or alters the native system in any way (Simberloff 2012). Whether a biological control agent could become problematic can be assessed with telemetry of individuals in a pilot study before initiating the intervention, and if there is limited risk of introducing a biological control agent, then this option could be a significant tool to help manage an invasion. A cursory search of Web of Science for articles in the focused journal *Biological Control* for studies integrating telemetry (searched for words relevant to telemetry [see methods for search string] in the *topic*) identified only one study among 2900 published in the journal in which electronic tagging was used to assess the effectiveness of a biological control agent.

Synthesis

Among the invasive animals studied with electronic tags and identified in this review, the most common organisms were large bodied invasive mammals and freshwater fishes (Fig. 3). However, there was a relatively limited diversity of species and there was high representation of a few focal species such as carps (Family Cyprinidae), salmonids (rainbow trout, brown trout), raccoon dog (Family Canidae), and American mink (Family Mustelidae; Fig. 3). Invasive crayfishes were also frequent subjects of tracking studies, even though there was a relative underrepresentation of invasive invertebrates. Poor representation of invertebrates most likely arose as a result of difficulties with tagging or tracking small-bodied organisms (Cooke et al. 2004; Wikelski et al. 2007). These trends are characteristic of invasion biology, in which animals that are easiest to observe are overrepresented (Lodge 1993). Presently, even with tools such as electronic tags, it is often impractical to monitor invasions of small-bodied organisms because of difficulty tagging these animals without excessive interference to the individual's biology (Cooke et al. 2004). Kissling et al. (2013) identified difficulties with using electronic tags to study insects, many species of which are prominent invasive species and pests (14 on the list of the worst invasive species; Lowe et al. 2000), but reviewed some examples of insect telemetry, some dating back to the 1980s. Smaller tags with better battery life and detectability are still needed to increase the applicability of electronic tags for tracking the spatial dynamics, habitat preferences, or competitive interactions of small-bodied animals to contribute to managing their invasions (Lorch et al. 2005). For aquatic invasive animals, miniaturization of acoustic transmitting tags has already created opportunities for tagging smaller individuals although this was not manifest in our findings, perhaps because miniaturization of electronic tags requires validation of tagging methods, especially as there is controversy about the appropriate body mass to tag mass ratio (Brown et al. 1999). In addition, small animals that seek complex refuges may be difficult to track (e.g., Cookingham and Ruetz 2008).

Even when appropriate technology is available, initiating tracking studies requires valid methodology for both animal welfare reasons (Kenward 2001) and to ensure capture, handling, and tagging do not alter behaviour and affect the interpretation of results. Moreover, identifying appropriate tagging methods is important to ensure tags are detectable (or retrievable such as for logging tags) and not easily lost. Nolfo and Hammond (2006) conducted a tag effects study on invasive nutria (*Myocastor coypus*), but found post-release predation of released nutria biased the results. To find the best method for tagging American mink, Zschille et al. (2008) compared intraperitoneal tagging to more traditional radio-collaring and recommended using internal tagging for long-term studies. In addition to validating tagging procedures, it is important to estimate detectability of animals as they may frequent complex environments where signals are difficult to obtain. Validating the effectiveness of tracking is especially important when using telemetry to study invasive species because false negatives indicating the absence of an invasive species can have important repercussions (e.g., Cookingham and Ruetz 2008). In some instances, the need to validate methods can render electronic tagging studies infeasible for studying biological invasions because it is often important to collect and analyze data quickly to create an action plan rather than expending limited resources validating methods.

Ethical considerations may restrict the viability of conducting electronic tagging studies on invasive species. Indeed, even though releasing non-native or invasive species can provide useful information, it is not necessarily good practice (Puth and Post 2005). For predictive studies, it may be necessary to identify the behaviour or physiology of animals in a new range, which may require the introduction of non-native species into a range where they have the potential to become invasive (e.g., Russell et al. 2008). To limit the risk that experimental animals will result in an unintentional introduction in a new habitat, controlled experiments can be conducted (e.g., Dawson et al. 2006) or individuals can be released into cages or enclosures rather than into the wild (e.g., Dorcas et al. 2011). However, these alternatives may reduce interactions between non-native and native species or introduce confinement stress that reduces the applicability of results. Releasing sterile individuals (e.g., Parkes et al. 2010) is a good alternative, permitting observations of animals in the wild. However, the use of contraceptives for sterilizing wild animals may be somewhat controversial (Thresher and Kuris 2004). When experiments are conducted on established invasive species, capturing, tagging, and releasing individuals can provide important information about the invasive population; however, there may be concerns about releasing invasive species back into the wild rather than destroying them. If only a small number of tagged individuals are likely to provide enough relevant information about an entire population, then potentially releasing a small number of tagged individuals of an invasive species may be justifiable. However, it is nonetheless vital to evaluate whether the likely benefits to be gained from the tagged individuals will exceed the potential costs of releasing them.

In some instances, non-native species are intentionally introduced either for biological control (see above) or for commercial or recreational purposes. Stocking non-native species into lakes is a form of intentional introduction for enhancing the economic value of a fishery and stimulating local economies. However, introduced species can spread rapidly (Thomas and Randall 2000) to adjacent watersheds either intentionally or incidentally (e.g., via birds or other predators). Non-native species may also be introduced as game for hunters (e.g., ungulates; Spear and Chown 2009). Given that not all introduced species are potentially invasive, telemetry can be used for identifying movements such as dispersal as well as to map interactions among the invasive and native biota including parasite transfer and competition to determine the invasion potential of introduced species (Table 2).

Electronic tags are popular for providing insight into otherwise cryptic ecological processes exhibited by animals, including interactions between an animal of interest and its biotic and abiotic environment. The observations made possible by electronic tags are of particular relevance to studying biological invasions because they provide crucial data that may allow swifter decision-making and action, particularly when time is a limiting factor. The data collected from electronic tags also provide a broader context for animal behaviour and interactions rather than the snapshots in time provided by tracks or markings that provide limited evidence of behaviour or ecology. When tagging efforts focus on multiple species (i.e. native and invasive) it is possible to identify habitat overlap and the potential for resource competition or antagonism. Manual methods such as direct observation, identification of carcasses, or faecal/stomach samples make interpretation of interactions somewhat unconvincing, whereas tagging and tracking can provide more persuasive evidence of overlap and competition or antagonism and even provide a quantitative estimate of interactions based on spatial overlap, home range sizes, or seasonal dispersal/movements.

For the management of biological invasions, electronic tagging is useful to predict if an animal could become invasive. Moreover, electronic tags can facilitate tests of preventive or control measures (Table 2). There are increasing opportunities for researchers to use tags for identifying behavioural processes that contribute to invasion success, such as by identifying activity intervals, resting periods, and dispersal capacity (e.g., Henry et al. 2013; Llewelyn et al. 2010). For managing invasions, mark-recapture methods with external markers have limited predictive value when evaluating where to place traps or barriers, but can provide post hoc evaluations of success by measuring the proportion trapped or excluded. Overall, mark-recapture methods provide limited context relative to electronic tagging studies. Tracking electronically tagged invasive species can demonstrate where the animals frequent and indicate where and when traps may be effective, but also why they may be ineffective; for instance, animals may simply not be encountering traps (e.g., Bravener and McLaughlin 2013).

In several studies in this review, tagging was used to determine where and when invasive species were present, such as habitat preferences, home ranges, and movement patterns across seasons or life history stages. However, limited evidence of integration between physiology and telemetry were identified, even though physiological data provide important context to behavioural data. Indeed, there is increasing importance of field physiology to the study of animal conservation (Wikelski and Cooke 2006), and there are likely more opportunities for combining physiology and telemetry to study biological invasions. Physiological data can be relevant to many questions about invasions (Lennox et al. 2015), certainly for determining whether a non-native animal can persist in a new environment, providing context (i.e. temperature) for habitat use including movements, dispersal, or migrations, and to quantify sublethal effects of interactions between native and invasive species. Heart rate data loggers, for example, can provide a proximate estimate about stress status of invasive species, which can affect the behaviour or reproductive capacity of animals and provide an estimate of the invasion potential or sublethal effects of interactions between native and invasive species. We found in our review that biologging devices are beginning to contribute to space use estimates for invasive animals, for instance using time-depth recorders to identify dive behaviour of invasive mink (Hays et al. 2007) can provide information about space use and potential interactions with other species. Although use of biologging devices for invasive species research appeared to be rare based on the results of this review (Fig. 2), there is considerable opportunity for further integration that will provide more information for managers about spatiotemporal habitat use by invasive species that can be capitalized on for control efforts.

Conclusion

Who, what, where, when, why, and how? These are the questions posed by conservation researchers and wildlife managers in a time when invasions, and a corresponding need for management, are increasing (Hulme et al. 2009). Managing invasive species is a logistical challenge for conservation practitioners because these species can establish in new habitats and spread rapidly. We submit that electronic tagging provides opportunities to answer these key questions about invasive species and facilitate proactive measures against the introduction, survival, reproduction, or spread of non-native species within local environments by remotely monitoring the biotic and abiotic interactions of both the native and non-native species. Evidence-based risk assessment and management of biological invasions are important for identifying effective options for controlling invasions, a trend that

Box 1 In this review, we identified four major ways in which electronic tags contribute to the study and management of biological invasions: (1) identifying spatial ecology of invasive species, (2) evaluating interactions between native and invasive species, (3) predicting invasions by quantifying invasiveness, and (4) developing or evaluating the effectiveness of control or management strategies. We present case studies for prominent invasive species for each to illustrate the ways in which electronic tags contribute to the study of invasive species

Identifying spatial ecology of invasive species from electronic tagging data

Several crayfish (Class Malacostraca) species have been introduced via ballast water or deliberately by anglers as bait and have become invasive species. Either to quantify invasiveness of a foreign species or to develop control options, monitoring spatial ecology of invasive species provides important insight into any biological invasion. Electronic tags applied to invasive crayfishes have provided relevant insight by allowing researchers to calculate home range sizes of adults and juveniles (Loughman et al. 2013) and contributed to identifying active periods during the mating season (Buřič et al. 2009) that can be exploited by implementing trapping programs. Using electronic tags to quantify habitat use of invasive animals can be used to predict competitive interactions, model rate of dispersal and spread, and also to set up barriers or traps that can be used to limit spread or persistence of the species

Elucidating interactions between native and invasive species from electronic tagging data

American mink *Neovison vison* have successfully established and become invasive in Europe and South America and have become abundant predators for native species. Tagging and tracking movements of invasive mink in conjunction with native prey species has provided information about interspecific interactions between native species and invasive mink (Carter and Bright 2003; Zschille et al. 2014). Medina-Vogel et al. (2013) identified niche partitioning arising from competition between invasive mink and native southern river otter *Lontra provocax*. Brzezińsk et al. (2012) tagged minks and native waterfowl and found that antagonism by minks was low among birds that lived near human developments, indicating that a source population of birds could potentially be maintained. Electronic tracking data can provide evidence of interspecific interactions and be useful for determining which native species are at risk due to invasions

Electronic tagging data can help identify invasive traits and predict invasions

Burmese pythons *Python bivittatus* are non-native snakes imported for the pet trade that have become invasive species in South Florida. To evaluate whether the pythons could potentially spread farther north into habitats in South Carolina, Dorcas et al. (2011) released radio-tagged pythons into an experimental enclosure to monitor their habitat use and survivorship in the colder climate. Radio tags allowed the researchers to identify their movements and behaviour and implanted thermologgers logged their core body temperature. Radio tracking the pythons allowed the researchers to identify aberrant behaviour, which could be synchronized with body temperature from the loggers. Because the cold temperatures were lethal for the snakes, the true invasion risk was determined to be low in South Carolina. Predicting invasions is an important component of management, and electronic tracking of potentially invasive animals can help quantify the risk of an invasion in local environments

Evaluating invasive species control options from electronic tagging data

Common carp *Cyprinus carpio* are one of the world's worst invasive species (Lowe et al. 2000). Carp have been introduced from Asia and established in freshwater habitats throughout the world where they can negatively affect local fisheries and ecosystems. Controlling carp populations and excluding them from establishing in new habitats is an important conservation priority that can be facilitated by tagging and tracking carp to evaluate their interaction with potential control mechanisms. For large-scale exclusions, electric barriers can be implemented that eliminate fish passage (Sparks et al. 2010). Telemetry of 'Judas' individuals can also facilitate identification of aggregations for culling (Bajer et al. 2011). Incorporating electronic tags into pilot programs of management regimes or using them to identify aggregations can greatly enhance the success of invasive animal management. When invasive species have established, controlling or containing their spread is an important priority for minimizing damage. Electronic tagging can help develop and test methods that are most effective for reducing the negative impacts of an invasion

was evident in our literature search. Indeed, telemetry is useful for making accurate observations about habitat use, activity times, and home ranges of invasive species for both the intrinsic ecological merit, but also determining how effective management can be implemented, or whether it is necessary at all. Perhaps the most important application of electronic tags is to make direct observations that help develop or validate management interventions that aim to prevent or control invasions by quantifying the success of traps or barriers and determining where and when such interventions could be expected to be most effective. However, care must be taken because although electronic tags provide reliable information about animals, the knowledge gained in one region may not be applicable to an invasion in another location, even though the same species may be the culprit invasive in both regions. Increasing the number of studies with these applied objectives will make electronic tagging increasingly relevant to the study of invasive species. In coming years, miniaturization of tags, increased utilization of physiological and environmental sensors incorporated into electronic tags, and an increasing number of valid tagging methods for invasive animals will allow for more invasive species to be studied with electronic tags so as to identify appropriate management interventions.

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