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Research article

Predation research with electronic tagging

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Predation is a fundamental aspect of ecology that drives ecosystem structure and function. A better understanding of predation can be facilitated by using electronic tags that log or transmit positions of predator or prey species in natural settings, however, there are special considerations that must be made to avoid biased estimates. We provide an overview of the tools available for studying predation with electronic tags including the tag types and analytical tools that can be used to identify where, when and how prey are killed by predators. We also discuss considerations for experimental design when studying predation using electronic tags, including how to minimize effects of capture and tagging procedures. Ongoing innovation and integration of sensors for tags will provide more detailed data about the performance of tagged predators and the fate of tagged prey. Where analysts can effectively resolve the timing of predation using state-of-the-art tags and analytical tools, we foresee exciting advances in our understanding of animal demographics, evolutionary trajectories and management systems. Prospects to develop new tools and approaches for tracking predation while designing studies to more effectively limit bias are an important frontier for understanding ecosystems and addressing human–wildlife conflicts. Given great uncertainties about environmental change and intensifying conflicts between humans and predators, effective study designs integrating electronic tagging to study predation have a promising future in fundamental and applied ecology.

Keywords: biologging, biotelemetry, compensatory mortality, ecosystem-based management, natural selection, predation sensor

Introduction

Predation is a formidable ecological force structuring the spatial dynamics of biodiversity, the demographics of prey populations (Krebs et al. 1995) and the evolutionary trajectory of species (Bro-Jørgensen 2013). The top–down effects of predators on survival and behaviour of prey species (i.e. consumptive and non-consumptive effects) are one of the most difficult ecological processes to study. Consequently,

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there is continued interest in advancing concepts related to predator–prey dynamics in nature, especially to understand why, when, where and how prey species overlap with predators and are being attacked by them (Smith et al. 2020, Suraci et al. 2022).

To learn more about predation, investigators observe attacks, track down kill sites, take stomach samples from predators, or use individual identifying marks to track predators or prey and study interactions (Ford and Ellis 2006, Ford and Clevenger 2010, Furey et al. 2021). One of the most promising research designs for predation is to observe predator behaviour, which has benefited from camera traps (Smith et al. 2020) and instrumentation of predators or prey with electronic tags to observe vital rates of prey (i.e. demographics), intake rates of predators, selection by predators and factors related to predator–prey movement ecology. Whereas camera traps focus on untagged individuals, tagging provides much higher resolution individual-scale data and the capacity to address a different suite of questions. The use of electronic tags has become an indispensable method for investigating the behaviour and life history of animals on land, in air and underwater (Hussey et al. 2015, Kays et al. 2015). Tracking animal paths using global positioning systems (GPS), reverse-GPS by positioning with receivers at known locations (e.g. radio and acoustic telemetry; Nathan et al. 2022), or light-based geolocation, as well as reconstructing networks from detection data (Whoriskey et al. 2019), has dramatically advanced our concept of animal ecology (Lowerre-Barbieri et al. 2021). These tagging procedures include instrumentation with both biotelemetry and biologging devices, the former devices transmitting data to receivers whereas the latter log data onboard to be downloaded upon recovery (Cooke et al. 2021). The resulting movement data can reveal if, when, where and sometimes how individual animals perform as predators and prey in a system (Klinard and Matley 2020, Lennox et al. 2021b). Several reviews address the use of electronic tags for aspects of ecological inquiry, including to address animal mortality (Klinard and Matley 2020, Villegas-Ríos et al. 2020); however, studying predation requires more specific considerations and designs.

An important and poignant question is whether new electronic tagging tools that are now available to researchers can help answer some of the major outstanding questions in ecology relevant to predator–prey systems. For example; how many animals are ultimately killed by predators, and for what share is this the ultimate compared to the proximate cause of death? How do human landscape changes and restoration efforts contribute to predation (Berekijian et al. 2016, Boulêtreau et al. 2018, Lennox et al. 2022a)? Is predation compensatory or additive upon prey populations (Linnell et al. 1995)? How does predation mortality scale with prey density (i.e. functional response)? We argue that the answer to these questions lies in the intersection between these new technological innovations and optimizing the study designs to get the most information out of each animal that is used in these studies. Here, we discuss current state of the art methods for studying both terrestrial and aquatic predator–prey research using animal tracking with electronic tags and provide a framework for effective study designs that address major shortcomings and potential biases.

Approaches to generating predation data from electronic tagging

Electronic tagging devices

Tagging individuals with biotelemetry or biologging instruments greatly expands the capacity with which analysts can draw conclusions about predation at the individual scale. Biologging devices can be attached to animals to record and store large amounts of data, often exceeding what can be transmitted. Biologgers include animal-mounted cameras (Heithaus et al. 2001), audio recorders (Studd et al. 2021) and high frequency tri-axial accelerometers (Viviant et al. 2010). Loggers can also store high frequency data on heart rate, orientation and other details about the individuals (Rutz and Hays 2009). Transmitters measure many similar quantities for animals, except transmissions are data-limited; in addition, data are only accessible if the tag is within range of a receiver that can log the transmissions. Receivers can be placed at fixed stations and downloaded when convenient, or operated manually by an investigator on foot or by vehicle searching for a tag to identify a position and estimate the fate at a given interval (Brodie et al. 2013). Transmitters are often used for species whose tags cannot easily be recovered. If tags are linked to satellite or mobile platforms, investigators can access data on their animals in near real time, potentially allowing rapid identification of mortalities and trips to check carcasses for signs of predation including prints, teeth marks, etc. Otherwise, manual tracking of transmitters will only allow fate determination at opportunistic intervals. Logging tags that are recovered must be downloaded after the fate of the animal is known (unless the logger fell off the animal) and downloaded to check where and when mortality occurred (Fig. 1).

Analysts can tag predators, their prey or both simultaneously. Prey species are more abundant than their predators and are therefore more readily available to be captured or trapped and instrumented with tags. Shorter lifetime of many prey species compared to their predators should be considered in study designs. Tagging predators may provide longer time series both because of longer lifespan and larger body size for tags with longer battery life. Where possible, tagging both predators and their prey can be effective for simultaneous observations (Fig. 1).

Analytical tools

Animal behaviour
Data from tags that transmit or log locations can be reconstructed to reveal behavioural patterns of predators and prey. Short interval sequences of positions can provide movement paths that describe where and when animals are active, what
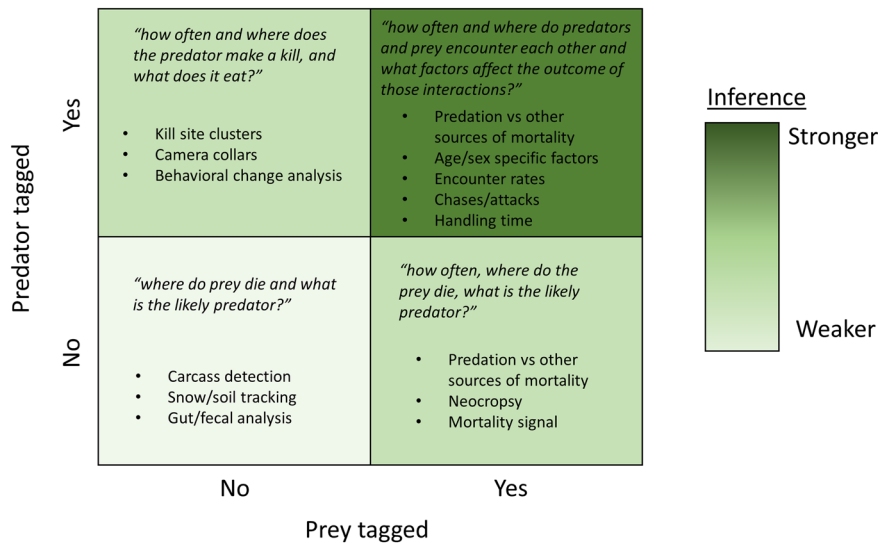
Figure 1. Questions addressed by tagging predators and their prey in a telemetry study. Weak inference is possible without individual tagging but stronger results can be obtained with electronic tagging.

habitats they are found in, their movement speed and trajectory, and turning angles and turning frequency (Signer et al. 2019, Nathan et al. 2022). A priori hypotheses about the movement tracks of a tagged animal can be compared to observations to identify anomalous patterns and infer whether it has been killed or has killed another animal. For example, step lengths between consecutive positions indicate changes in movement speeds (Carter et al. 2020), and could be applied to infer whether a tag has been consumed by a larger animal. Predators may also have notable turning patterns indicative of a foraging mode (Franke et al. 2006). These analyses can be carried out using Hidden Markov models that use step lengths and turning angles from movement paths to discern states (McClintock and Michelot 2018, Runde et al. 2020). An additional task may be required to cluster behavioural patterns from a tag to identify individuals that have been eaten. Studies such as these have been rare within field ecology. However, the broader use of high-resolution GPS and acoustic telemetry in ecology and wildlife management is making such studies more feasible. High-throughput tracking systems such as ATLAS (Beardsworth et al. 2021) and four-dimensional acoustic telemetry arrays in aquatic environments (Lennox et al. 2021a) provide study designs that can greatly advance our understanding of predator–prey behaviour in field contexts using such big data approaches (Krause et al. 2013, Nathan et al. 2022).

When continuous path data are not available, analysts can use detection data to quantify movement patterns and evaluate the fate. Selecting which behavioural metrics to use is somewhat post-hoc and requires consideration of the potential predators involved. Summary statistics of network analysis describing betweenness, closeness, degree and other graph theory metrics will provide an indication of how animals are using space in an area and whether these patterns correspond to expected patterns of the tagged animal or not (Whoriskey et al. 2019). Gibson et al. (2015) and

Daniels et al. (2019) both investigated acoustic telemetry detections of Atlantic salmon *Salmo salar* smolts to estimate whether they had been eaten by striped bass *Morone saxatilis* from detection data. Striped bass behaviour was known from simultaneous tagging to quantify behavioural patterns expected of the predators, which was determined to be distinct from the salmon smolts. Supervised machine learning models were tuned to assign a class of eaten or not eaten to the smolts. Gathering data on the movement of dead animals (Muhametsafina et al. 2014) may be necessary as a negative control; dead animals may drift with water currents or be carried by scavengers and the patterns of these movements are useful to train some classification tools (Runde et al. 2020, 2021). These behavioural metrics may be insufficient to resolve all predation events, especially if predator and prey behaviour are difficult to separate. In Norway, Lennox et al. (2021b) described acoustic telemetry tracking of Atlantic salmon smolts simultaneous with predatory brown trout in a lake, where spring migration of the smolts and sea trout had very similar behavioural patterns, making behaviour ineffective to consistently identify smolts that were eaten without specialized sensors for detecting predation (Box 1).

Animal physiology

Physiological markers that distinguish predation events, monitored by electronic tags, can be used for investigating predation for both predators and prey. Local temperature is a key tool for monitoring predation. In predators, temperature sensors have been placed in the stomachs of bluefin tuna to measure local gut heat and thereby identify feeding locations and times; these data were then used to suggest areas to protect critical habitat (Whitlock et al. 2015). Abrupt temperature changes for similar local temperature sensors have the potential to identify predation of a tagged prey. For example, temperature loggers can be used to detect predation events where the predator's core temperature is known to be different from

Box 1. Case studies of electronic tagging research as a method for studying the natural predation dynamics of animals in field studies.

Atlantic salmon were tracked in the Norwegian river Aureelva with radio tags and temperature loggers. Tracking allowed recovery of tags brought on land by Eurasian river otters *Lutra lutra* and the date and time of predation was ascertained by matching the temperature logger with values from a temperature station on land and in the river.

Predation sensor transmitters implanted in Atlantic salmon smolts in the river Vosso, western Norway provide details about the fate of the fish during their seaward migration. Predation sensors have an internal state machine and transmit orientation data to receivers so that analysts can track behaviour and fate at different phases of the migration (Lennox et al. 2021a).

Killer whales were instrumented with GPS satellite tags. Whales were found to follow the herring southerly migration along the coast from their inshore overwintering areas to offshore spawning grounds. Additionally, herring density was found to impact the whale horizontal movements (Vogel et al 2021).

Cluster patterns in GPS locations for a cougar *Puma concolor* combined with mortality signals on a collared mule deer *Odocoileus hemionus* indicate the timing and location of predation. In some cases, cougars are displaced from kills by other predators, and only by having collars on both species do we understand how important these predator–predator interactions might be. [photo credit Siobhan Darlington]

the tagged animal (Tolentino et al. 2017, Strøm et al. 2019, Gallagher et al. 2021). Atlantic salmon kelts tagged with temperature-sensitive archival tags revealed predation based on rapid temperature warming attributed to cetaceans and endothermic fishes. Another animal physiological indicator is the use of pH-based sensors that can be used to indicate whether the animal has been digested in the stomach and intestines of the predator (Halfyard et al. 2017, Hanssen et al. 2021).

Animal location

A tag's location can provide information about an animal's behaviour and fate. When detailed habitat information is available from a study area, such as raster data on canopy cover, grass height, substrate class, etc., then tag position may be used to inform about resource selection and evaluate what fraction of the time the tag is found in its expected habitat or if the tagged animal is selecting an unusual habitat. Resource selection function models (Avgar et al. 2016) may be effective for estimating this, and unlike alternative methods, may help identify the predator species if a priori data are available on resource selection by candidate predators, for example based on simultaneous tagging of predators, historical data or local knowledge. After death, recovery of tags may be used to determine whether the tagged animal had been eaten. Tags recovered in predator dens or nests can indicate that the tagged animal and its tag were eaten and brought back by a central place forager (Skov et al. 2014, Blythman et al. 2017). Scanning for passive integrated transponders using handheld readers or manually seeking radio tags to place them at or around predator nesting sites can provide some resolution on the fate of tagged animals, although investigators may wonder whether a predator scavenged a carcass or killed it itself. Ford et al. (2014) quantified per capita risk of mortality of predation to assess top–down forcing through a food web in an African rangeland. Per capita risk quantifies the amount of time prey spends in an area (or habitat type) relative to the proportion of carcasses found in the same area. Similarly, Ali et al. (2017) assessed per capita risk of mortality to link rangeland degradation to the population dynamics of the critically Endangered hirola antelope *Beatragus hunteri*.

Important consideration when designing telemetry studies to study predation

When tagging prey, analysts will need to know what information could be used to identify if, when, and where the tagged animal has died and whether deaths can be attributed to predation or to other factors. Selecting tags with mortality or predation sensors can help with this task, along with additional sensors like temperature or depth/elevation sensors. Recovery of tags tracked back to kill sites or nests/dens can be useful to identify predators with greater certainty, as can tracing back predator tracks. Determining which predators are responsible for killing tagged prey is challenging but important, few tags are available to help with this other than critter cam biologgers and audio recorders that are heavy, expensive, and impractical for small prey species. Analytical tools may assist in identifying behaviour of the tag after predation to determine whether movement patterns, internal temperature or overall activity is indicative of a certain predator. However, these will optimally be calibrated from simultaneous observations of tagged predators (Gibson et al. 2015). Finally, investigators must plan whether the sample will provide enough data from the tagged population to test hypotheses about predation. Tagging a large proportion of a prey population is challenging but necessary if conclusions are to be drawn about the share of mortality attributable to predation in a population, selective predation or other relevant ecological hypotheses are to be tested.

When tagging predators, investigators must make similar experimental accommodation. Capture of predators should be representative of the sampling population and consider how predation behaviour will differ between sexes and at ontogenic stages. Depending on resource availability, it may be necessary to spread tags evenly or focus on one sex/ age class. Tags must have sufficient resolution to identify predation events in the data (Irvine et al. 2022). Identifying prey from predator tracks will be challenging but predators are often large enough to use critter cam biologgers and help train movement algorithms to identify hunting patterns based on movement patterns and habitat selection. When calculating predation rates, researchers should consider whether predation activity will be biased by the use of such heavy or burdensome tag packages or anaesthetics that reduce performance.

Biased sample

Gear used to capture individuals for tagging may favour certain morphological and/or behavioural traits, resulting in a biased sample (Biro 2013). For aquatic species, individuals with certain body size and morphology may be more easily caught by gear and then overrepresented in instrumented samples. For instance, fish with larger mouths are more susceptible to ingest hooks or lures compared to individuals with smaller mouths (Alós et al. 2014). Certain behavioural traits may also affect an individual's likelihood of encountering fishing gear (Lennox et al. 2017). Both theoretical and empirical evidence suggests that more active and exploratory animals have a greater likelihood of encountering fishing gear, consequently such fish may be overrepresented in some fish telemetry studies (Alós et al. 2012). Preferential selection of individuals with certain behavioural traits have also been found with elk *Cervus canadensis*, where harvested elk moved faster and chose open areas, increasing their detectability to hunters, compared to surviving elk who moved more slowly and avoided open areas (Ciuti et al. 2012). Capturing individuals prior to tagging will therefore depend on their individual traits, and individuals that are cautious and harder to find may be underrepresented in telemetry studies with implications for understanding predation rates and selection. Researchers may also introduce bias by preferentially tagging healthy individuals that may be less vulnerable to predation than malformed or infected counterparts (Arreguin-Sanchez 1996), which would be more vulnerable to predation.

Approaches to sampling using mixed gear methods should be favoured to ensure a sample is as representative of the prey population as possible (Michelangeli et al. 2016).

Experimental procedure effects

Tagging an animal involves capturing, restraining (which may include anaesthesia), and a mechanical tagging procedure on the individual before it is released (Kays et al. 2015, Brownscombe et al. 2019). The process of handling and tagging may alter behaviour and reduce fitness in the tagged animals for some time after tagging, possibly affecting their probability of being killed by predators (Olney et al. 2006, Brown et al. 2010, Raby et al. 2014, Wilson et al. 2017). For example, Sonamzi et al. (2020) found a clear difference in activity of radio tagged tigerfish *Hydrocynus vittatus* up to one week after tagging before recording three eventually being eaten. Attaching tags externally may be considered to be less invasive than surgical implantation, reducing tag effects, but drag or visibility of the tag should be considered potential confounding factors. Predators often target weak and injured individuals because they are easier to catch, so individuals affected by capture and handling are expected to be more vulnerable to predators (Jenkins et al. 2004). Post-release predation of stressed animals will then be especially high where predator burden is intense (Raby 2014). Mechanisms of action for this elevated predation risk include byproducts of stress perceptible to predators (e.g. metabolites released into water; Dallas et al. 2010). Holding tagged animals for recovery after tagging may attenuate or exacerbate stress and investigators should be familiar with suitable options that will allow physiological recovery following surgeries when calculating predation rates using tagging data.

Some study designs require additional samples of the animal that can be used to ascertain physiological state or disease profile for linking to fates such as predation. Biomarker information derived from these live biopsies of hair, scale, mucous, saliva, blood, gill, muscle or other tissue may be crucial to understand the underlying selection processes that drive predation. Sampling protocols are well established for many species but variation in sample volume can have a variable effect on animal condition after undergoing a procedure. The additive or synergistic impact of the additional stress imposed on the animal by combining biopsy with tagging is important for investigators to consider. For example, Bass et al. (2020) demonstrated that survival of tagged sockeye salmon smolts were lower when the researchers had taken an additional gill biopsy of the fish. The gill samples would provide details about the animal transcriptome relevant to understand predator vulnerability and selection, but the added physiological cost would confound conclusions that investigators may attempt to draw from these data as a consequence of the procedural effect.

To reduce negative impacts imposed by stressful conditions (e.g. handling and tagging), animals are tagged using anaesthetics and analgesics (Young et al. 2019). Common anaesthetics for fish include tricaine methanesulfonate (MS-222), clove oil, 2-phenoxyethanol and benzocaine (Ross et al.

2008). Free-ranging terrestrial animals are often chemically immobilised using remote-delivery systems (e.g. free-range darting) and combinations of drugs (e.g. medetomidine–ketamine, xylazine–ketamine) to achieve balanced anaesthesia (Caulkett and Arnemo 2007, Brivio et al. 2015). Ventilation with isoflurane or sevoflurane may be preferred as anaesthetic for longer procedures (Caulkett and Arnemo 2007). Anaesthetics reduce the stress response of animals exposed to handling and tagging but the compounds remain circulating in the animal's system until metabolized, possibly affecting the brain's ability to discern predators or the muscular capacity to escape. How long an anaesthetic remains in the system varies with anaesthetic type and species. For Atlantic salmon, MS-222 is eliminated fastest among common anaesthetics with abody clearance rate of 3.096 l kg^{-1} h^{-1}, followed by Benzocaine (0.348 l kg^{-1} h^{-1}) and Isoeugenol (0.059 l kg^{-1} h^{-1}; Kiessling et al. 2009). The choice of anaesthetic when studying predation should be taken into consideration before the study to reduce the time period during which tagged individuals have higher risk for predation, and the effect of anaesthesia should be accounted for in the analysis of results. Whether to hold animals for clearance of anaesthetic will depend on the stress response of the animal to the holding conditions. Large semi-natural enclosures may be useful for providing a safe space for anaesthetic recovery prior to releasing a tagged animal back to a predator–rich environment.

Tag burden

Tag burdens may directly affect behaviour of instrumented animals, biasing predation estimates. Collars around the necks of animals may alter their behaviour, for example cats instrumented with heavier collars had smaller home ranges (Coughlin and van Heezik 2014). In fish, the swimming strategy and performance are reflected through adaptations in their body shape (Webb 1984). Drag imposed by external tags have shown to reduce the critical swimming speed in both externally tagged Atlantic cod *Gadus morhua* (Steinhausen et al. 2006) and externally tagged juvenile masu salmon *Oncorhynchus masou* (Makiguchi and Ueda 2009). The use of PSATs on European eel *Anguilla anguilla* have indicated that the drag effect had a greater impact on their swimming efficiency rather than the additional buoyancy from the tag (Burgerhout et al. 2011). Often, external tags may be preferred to reduce the need for invasive procedures, but analysts should consider whether external tags will increase vulnerability of the animal and bias results based on tag size and placement.

Tag detectability by predators

Tags should be as small as possible and neutrally coloured based on the placement of the tag to avoid visual betrayal. If not, the visible tag can make prey more susceptible to predation, which might be the case in a tagging study conducted on eight American eels *Anguilla rostrata* (Béguer-Pon et al. 2012); three of six externally instrumented individuals taken

by predators within two days. It is ideal if external tags are concealed and undetectable. Even though predators do not see tags, they may hear tags that are transmitting within their auditory range. The 69 kHz frequency is commonly used in acoustic tags (Reubens et al. 2021), and Bowles et al. (2010) found that some seals and small cetaceans can hear sound emitted at this frequency, forming the basis of the dinner-bell hypothesis that acoustically tagged animals are more vulnerable to predation. Grey seals *Halicherus grypus*, for example, can hear acoustic tags and seem to be able to use the signals to locate food (Stansbury et al. 2015). In a field study, Chinook salmon *Oncorhynchus tshawytscha* tagged with acoustic tags in the USA had a significantly lower survival rate compared to individuals that were tagged with sham (inactive) acoustic tags and those tagged with only PIT tags (Wargo Rub and Sandford 2020). These findings highlight how tag choices can affect outcomes when aiming to study predation in the wild and bias the calculation of vital rates.

Addressing major ecological questions with predator–prey tagging

Predation is fundamental to ecology while also having important applied aspects relevant to mitigation of human wildlife conflict, fish and wildlife population management strategies, epidemic control and spatial management. Manipulative and mensurative experiments have historically been conducted to investigate demographic responses of animals to predation risk and the direct impacts of predation on population demography (Krebs et al. 1995) and less visible concepts have been unravelled using tagging to understand landscapes of fear, energy landscapes and their combination (Gallagher et al. 2017). Experimental approaches to investigate fundamental aspects of predation have had an important role in determining how predators and prey respond to cues and subsidies with camera traps (Smith et al. 2020) but the individual resolution provided by tagging can open new and broader research avenues not possible with imaging. Studying the direct effects of predators on prey populations has been poorly developed because of how difficult it is to observe predation in the wild without tools for constant individual surveillance. To wit, there are many research questions that have historically been impossible to resolve that are now much more accessible with the tracking hardware and analytical tools available to investigators. Here, we present a series of research questions and use our research framework to illustrate how electronic tagging can help address some of these pressing ecological questions.

How important is predation as a proximate and ultimate cause of mortality?

Does predation cause additive or compensatory mortality of prey?
One of the most important questions in predation ecology is whether prey dies as a consequence of the predation event or if the prey is eaten because it is about to die from another factor. Compensatory mortality may occur on relatively short time scales where the prey is imminently moribund due to disease or injury, or may occur across seasons due to density dependence or other population factors (Boyce et al. 1999). There are several study designs using telemetry that can research insights into these mechanisms; of particular interest is exploiting the individual data that telemetry provides. Correctly describing the individual variation in traits or condition status can allow researchers to assess whether these traits correlate with likelihood of predation, and whether these same traits correlate with mortality when predation pressure is attenuated. Observational studies can be useful to help calculate additive and compensatory mortality; however, experimental approaches may be much more powerful. Experimental manipulations of prey, for example, can help reveal whether predation risk is enhanced by contextual factors or whether prey can buffer added risk by behavioural or physiological flexibility. Herting and Witt (1967) used such a manipulation to study whether stress and injury enhanced predation by a predator in aquaria, but such designs would be much more effective when tracking animals in the wild under realistic contexts. Replicated ponds or enclosures can also be used to vary predator and prey density while manipulating prey condition (e.g. with stress implants; Sopinka et al. 2015). Tracking individual fates can then be used to test how predation may contribute to prey demographics.

Is predation selective?

For sick or diseased individuals?
Selective mortality follows the healthy herds hypothesis and sanitation effects, such that predation reduces the spread of etiological agents that have a strong effect on prey populations (Packer et al. 2003). Efforts to directly quantify predator selection for diseased animals have, for example, compared disease before and after predators were reintroduced (Barber-Meyer et al. 2007) and compared disease rates of the population mean to that detected in individuals removed from predator stomachs (Furey et al. 2021). Direct tests can be accomplished by tagging a random population sample, screening for disease and determining the fate of the individuals to model predation risk as a function of disease. Mensurative designs will consist of counting ectoparasites or using genomic methods to identify pathogen loads (Miller et al. 2014, Jeffries et al. 2021). Manipulative experiments combining experimental infections (Serra-Llinares et al. 2020) with tagging and release into areas with low or high predator burden may be particularly powerful to generate robust comparisons between treated and control groups with respect to mortality by predation or other effects of disease.

For specific prey traits?
Individual trait variation is an important feature of populations. Trait variation underlies resilience and flexibility to environmental change and can also be a bet-hedging

strategy wherein energetic investments in e.g. ornamentation or metabolic performance can be costly but highly beneficial (Godin and McDonough 2003, Robert and Bronikowski 2010). Hypotheses about prey performance and vulnerability to predation can then be unraveled with individual marking and fate determination. Predator trait selection must be an important component of ecological systems but is logistically challenging to identify without individual tagging and fate identification paired with phenotype classifications. There is evidence that predators are selective for prey size classes (Hulthén et al. 2017) and other traits like speed and crypsis must also have a role. A key challenge when tagging animals to study trait-based selection by predators is that capture methods are themselves selective, so traps and baits may result in biased trait distributions for tagging.

Does predation follow landscape features?

How does adherence to the landscape of fear affect survival probability?
The landscape of fear has been a powerful tool for describing non-consumptive effects of predators on the distribution and activity of prey. Electronic tagging studies have helped to reveal how prey species' distributions are affected by predation risk (Arias-Del Razo et al. 2012); however, few studies have extended this concept with direct observations of predation. The landscape of fear promotes vigilance among prey that minimizes but does not eliminate predation risk. Particularly in small areas such as islands or lakes, substantial overlap between predators and prey will influence how effective the landscape of fear is at the individual and population level. High throughput approaches to simultaneously track the movements of predators and prey while maintaining resolution to identify individual prey fates will help extend how effective landscapes of fear are for mitigating predation risk and how deviations may result in predation. Whole lake experiments, for example, can provide precise fish positions minute by minute. Whole-lake acoustic telemetry experiments combining, for example, tagging of predatory muskellunge *Esox masquinongy* with pumpkinseed sunfish *Lepomis gibbosus* instrumented with predation sensor tags (Lennox et al. 2021a) could be a design that could reveal not only how the predator and prey distribute in the lake, but also how prey movement choices affect probability of predation (reviewed by Lennox et al. 2021b). Replicated areas where the predator and prey densities are varied can provide a strong study design to investigate the landscape of fear.

Can habitat restoration modulate predation rates?
Landscape characteristics can play an important role in predation. Homogenous landscapes may increase prey visibility and reduce refuge. Ecological restoration frequently focuses on providing habitat and reducing density-dependent mortality of prey whose abundance is limited by suitable refuge. For juvenile Atlantic salmon, refuge in gravel interstitia, undercut banks and woody debris is important and thought to limit predation risk and restoration efforts have shown that remediating these habitat features can increase juvenile densities (Pulg et al. 2022). Direct tests have demonstrated that increased habitat complexity reduced predation (Miyamoto et al. 2021). However, mechanistic data to support restoration actions are often more difficult to obtain. Tracking predation risk in situ using electronic tagging can be viable to better ascertain how habitat availability is linked to predation risk and whether restoration can buffer predation and enhance prey abundance by increasing local carrying capacities. Tagging has already been presented as an important tool for supporting restoration (Lapointe et al. 2013) and tagging provides a strong link between restoration and predation.

How is predation linked to population density?

What is the numerical response of predators to prey density?
Holling (1959) introduced the functional and numerical responses as simple illustrations of the dynamic unfolding between predators and their prey as a predominantly density-dependent process. The idea that predators have both numerical and functional responses to prey has inspired much ecological inquiry (Abrams and Ginzburg 2000). Laboratory trials have used simple systems such as zooplankton to investigate predator handling time, satiation and the shapes of response curves. In larger study systems that are actually managed by humans, there is a great need to understand how predators respond to prey density. Furey et al. (2018) described migratory coupling as a response elicited by predators to prey migration and there are many important examples, including hatching sea turtles attracting mesopredators (Urbanek et al. 2016) and nesting geese attracting red fox *Vulpes vulpes* (Marolla et al. 2019). Managers know where and when these migrations occur based on phenological models but simple observations of predators at nesting or hatching sites will underestimate aggregative responses from the population. Tagging predators and investigating how their movements are actually altered to exploit these seasonal resource pulses is therefore necessary. Combining tracking with biologging tools such as accelerometers, critter cams and recorders can help attribute behaviour to predation activity (Machovsky-Capuska et al. 2016, Studd et al. 2021). Importantly as many management paradigms aim to remove predators to relieve predation pressure, tracking can reveal whether local immigration will rapidly replace individuals removed from sites. Indeed, local immigration can be a pitfall of predator removal that ensures it is neither sustainable nor successful to address the numerical responses of predators to migratory animals (Lennox et al. 2018). When instrumenting predators to calculate their numerical response, minimizing capture biases are crucial. Capture methods and locations may be key to determining aggregative responses within a predator population and failure to generate a representative sample will dramatically alter conclusions and management advice emanating from the experiments.

Is the functional response of predators to prey density a type III to type II?

A classic but complex question in conservation biology is whether the functional response between predator and prey a stabilizing type III functional response is where prey have a refuge at low densities or a destabilizing type II functional response where prey populations can go locally extinct (Hunsicker et al. 2011). In reality, this question is at its core a question of whether predators keep targeting, capturing and killing prey when prey populations are low. Predation telemetry studies are ideal for providing such insights into the behaviour of predators to give insights into searching behavior and the frequency of attacks by individual predators, while revealing whether prey animals are likely to change their behavior and risk taking frequency at different prey densities. In nature, functional responses are complex and sensitive to scale, meaning that individual tracking data can play an important role in better understand this predator–prey relationship (Gobin et al. 2022). Although FR are challenging data to enumerate, predation telemetry studies can be used to inform the scientist about the mechanisms that are at play when prey populations are in need of a prey refuge.

Can predation data help ecosystem-based management?

Are there problem predators in conflict areas?

Predators are often cited as agents reducing the harvestable surplus of fish and wildlife desirable to outdoorspersons. Simply identifying which species are major predators can be challenging (Kissui 2008) but problem individuals can be even more challenging. Indiscriminate culling can be ineffective for addressing population-scale challenges; therefore, it is necessary to determine whether there are problem individuals in a population using identifying marks and especially using individual tracking. For example, Wright et al. (2007) used acoustic telemetry to identify a small proportion (0.125) of tagged harbour seals *Phoca vitulina* were specializing on salmonids based on their tendency to remain around the river. Management targeting seals would therefore need to be relatively selective to impact the rate of predation on coho salmon *Oncorhynchus kisutch* in that study because random culling would most likely remove a non-salmon specialist.

Are management interventions effective for population restoration?

One of the ultimate challenges for managers is to protect threatened populations and enhance depleted ones. Predators are occasionally viewed as a direct threat to conservation of threatened populations and non-lethal and lethal options may be explored. When prey populations fall into what is called a predator pit (Sinclair et al. 1998), there is potential that predation is limiting recovery potential. Lethal control of predators rarely works because of local immigration, which can be tracked with electronic tags; translocation of predators out of conflict areas may similarly be an ineffective alternative and tracking can help resolve if and when predators

return to their previous haunts (Linnell et al. 1997). Sensory distractions such as lights, sounds or smells can be used to used to deflect predators from sensitive areas and movement data from tags can be used to test whether such deterrents are indeed effective for altering predator behaviour (Adams and Kitchen 2018) as well as if they are useful to alter the number of prey killed by predators based on tagging.

Horizon scanning predation research with telemetry

Although the type of tags (acoustic, GPS, radio tags) that are used in animal tracking has remained similar over the last decades, miniaturization of tags and development of sensors that collect more detailed data on individual behavior now allow studies that were not possible before, particularly relevant to small prey species. Specific interest in resolving the fate of animals in aquatic ecosystems has advanced on mortality sensors in radio tags and yielded a predation sensor acoustic tag, a device with an integrated sensor that transmits the tagged animal's fate to receivers (Halfyard et al. 2017, Lennox et al. 2021a). The difficulties of validating data from such sensors will, however, require ongoing refinement that requires collaboration between technology developers and scientists (Notte et al. 2022). Specialized sensors for aquatic species offer promise as a tool that could be developed and integrated into other tag types used on terrestrial animals, which has the potential to support further advancement of predation research using telemetry. Biologgers such as cameras or audio recorders (Studd et al. 2021) offer great promise for insight into the behaviour of predators and identifying predators and prey for larger species that can manage to carry such devices, and where they can be recovered for analysis (Machovsky-Capuska et al. 2016).

Technology that can support predation data from telemetry will continue to develop, including such techniques as eDNA to swab recovered tags and more molecular methods for prey biopsies to understand genotypes and phenotypes of prey and how these relate to selection (Miller et al. 2014, Peelle et al. 2019). The development of more specific genetic markers and utilization of new types of PCR methods such as droplets digital PCR (Allan et al 2021) methods will enable scientists to generate increasingly accurate links between prey and predators from non-invasive material such as saliva (Peelle et al. 2019). In parallel, identification of genetic markers that allow analysts to identify physiological state based on small biopsies will allow analysts to couple predation events with physiological state, facilitating insights into how compensatory or additive mortality operates within populations of prey as tagged animals are progressively determined to succumb to predation. Handheld PCR machines may support real-time field allocations in mensurative experiments aiming to compare groups based on genomic signatures (Marx 2015). Although pairing biopsies with telemetry generates myriad opportunities for scientists, this also requires standards be developed for best practice using multiple methods

and better understanding of how biopsies affect prey behaviour and mortality risk (Bass et al. 2020). We foresee a future where there will be an exponential growth in the use of advanced sensory and molecular methods to study predation using telemetry.

Analytical tools are increasingly available for tracking movement ecology (reviewed by Joo et al. 2020). Tools for identifying animal state and behaviour from movement tracks have become popular (McClintock et al. 2020) and step-selection functions (Signer et al. 2019). These analytical tools have potential to be increasingly refined and applied to the detection of predation for free-ranging animals based on state changes in behaviour. Manual methods have been applied successfully by Gibson et al. (2015) and Daniels et al. (2019), including refinements by Notte et al. (2022). Principles for identifying predation from movement can be extended from the accelerometer-based state machines integrated into acoustic tags (Lennox et al. 2021a) that identify sudden and persistent changes in behavioural states indicative of a state change in the carrier of the tag. However, this will only work for animals that are fully consumed and carried around by the predator for some time. Confident attribution of fates including predation represent a major and important step forward, and may benefit from greater use of negative controls that ground-truth the movement patterns of tagged animal carcasses (Runde et al. 2020, 2021).

The increased use of telemetry technology that can simultaneously survey predation events also comes with ethical dilemmas. Some tagging methods are likely to increase the likelihood of predation (Korpimäki et al. 1996). Animal welfare committees and ethics boards may consider experiments observing predation to be unethical in some cases. Refinement, replacement and reduction will always be important in animal tracking studies. And as with other studies, the urgent need for predation studies should be considered in light of their importance to understanding ecological systems and addressing conflicts against the potential for undue harm caused by capture, handling and instrumentation.

Synthesis

There is a diverse toolbox available to study predation; Smith et al. (2020) reviewed some of the experimental designs that can be paired with passive camera trapping, for example.

Box 2. Predator conflicts with salmonids are a salient example of using telemetry to reveal vital rates, functional and numerical responses, and compensatory/additive mortality of predators in systems around the world. Photograph credited to Vegard Lødøen (<www.vlfoto.no/>) and reproduced with permission.

Conflicts between predators and important fish stocks are a typical challenge for management. Migratory fish such as salmon (*Oncorhynchus* spp., *Salmo salar*) cross boundaries and are vulnerable to predators at all life stages. Density-dependent mortality of salmonid fry is attributable to predation and migratory smolts are known to aggregate birds (Skov et al. 2014), freshwater fish (Kennedy et al. 2018) and marine fish (Hedger et al. 2011). At sea, salmon are eaten by sharks, cetaceans and large fish (Strøm et al. 2019). Upon returning to coastal areas, salmon are targeted by whales, seals and sharks and in rivers by bears and otters.

Understanding predation dynamics of salmon has benefited greatly from electronic tagging. Analytical tools (Gibson et al. 2015), field protocols (Skov et al. 2014) and tag technologies (Halfyard et al. 2017, Lennox et al. 2021a) have been developed to assist calculations of predation to identify predation hotspots and bottlenecks for salmon smolts (Hanssen et al. 2021). Combining tagging with biopsies and trait measurements has provided evidence for selective predation (Miller et al. 2014). Tagging of predators such as trout *Salmo trutta* and cod *Gadus morhua* has helped identify co-migration of predators to exploit smolt migrations (Hedger et al. 2011, Lennox et al. 2019) while tagging seals helped Wright et al. (2007) identify specialization of some seals *Phoca vitulina* to feed on returning adult salmon. Sortland et al. (unpubl.) developed a tag package to calculate the number of salmon taken by otters and determine whether otter predation was additive or compensatory in a threatened population. Conflicts between predators and salmonids are not likely to disappear anytime soon, and tagging is likely to provide new opportunities to test predation deterrents and refine calculations of vital rates for these animals.

However, no tool provides quite the strong level of inference as individual tagging with electronic tags. Where researchers are interested in manipulative experiments via altered densities, individual conditions or traits or interventions (e.g. sensory cues to deflect predators), there is a strong potential role for using tagging. The value of tagging and the high resolution of individual behaviour, physiology and life history from logged or transmitted data will always have to be balanced against concerns of sampling bias, costliness of capture and instrumentation, and animal welfare concerns. Tagging can also be combined with other approaches such as camera trapping to generate powerful approaches through mixed designs that help better understand ecological systems. Therefore, tagging is not necessarily the ultimate tool for studying predation but a powerful one with many potential applications. However, we foresee that the great power of these tools to test challenging ecological hypotheses will lead to a dramatic increase in the use of these technologies in the near future (Box 2).
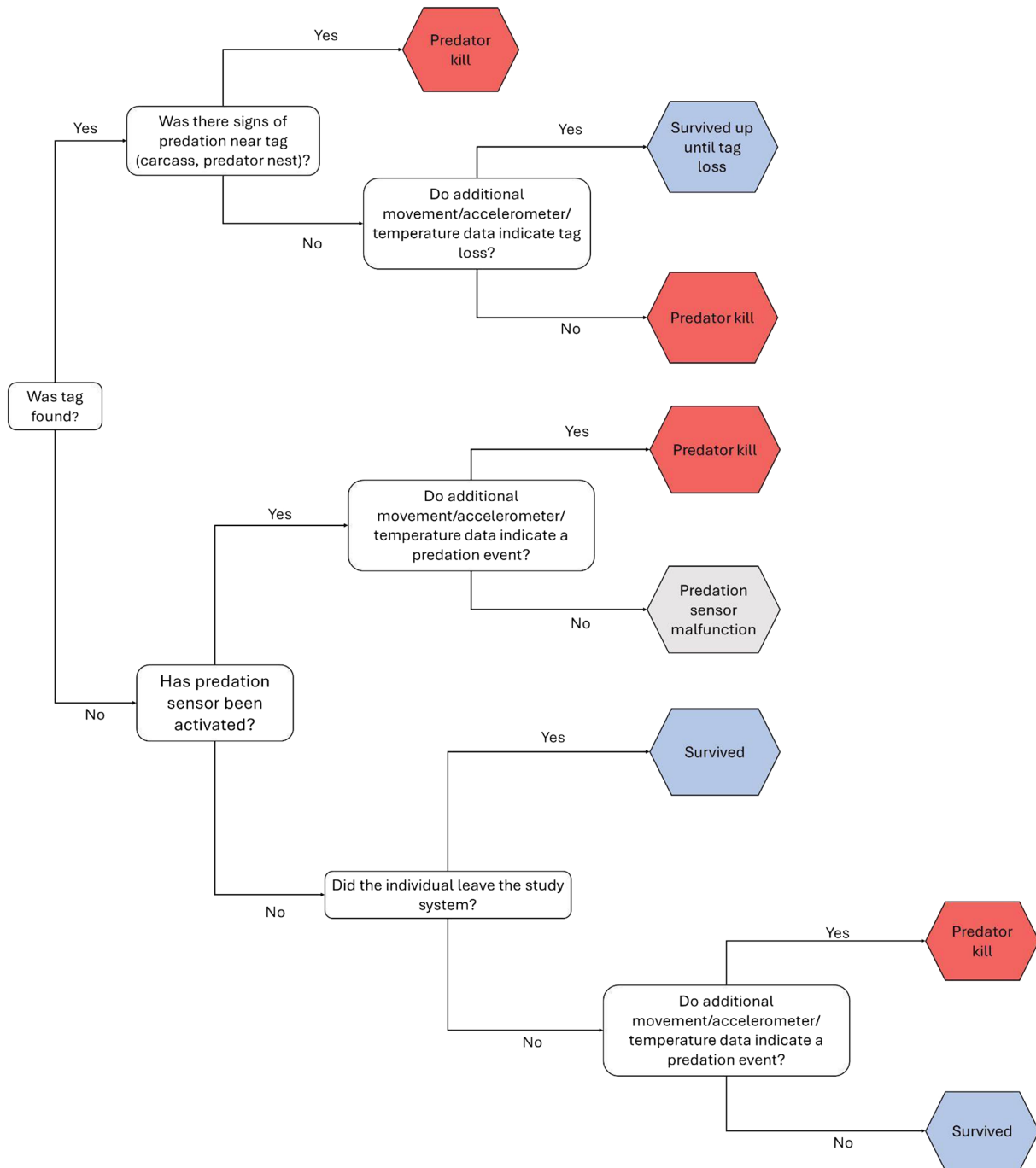

Figure 2. An example decision tree that can be used for categorization of fates in predation-telemetry research.

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In the corpus of electronic tagging research, direct efforts to understand predator–prey dynamics offer an exciting frontier for further research (Box 1). In many contexts, predation of tagged animals is an inconvenience to research when tags start to misbehave or disappear from study areas and these anomalies require some explanation or exclusion (Béguer-Pon et al. 2012). Efforts to separate a tagged species from a predator can be a nuisance when attempting to model behaviour of the prey species and error is introduced by incidentally modelling predator behaviours (Fig. 2). We have provided some insight into the present state-of-the-art for identifying predation events in telemetry data including statistical models for classifying tags that have been eaten (Gibson et al. 2015, Daniels et al. 2019), specific tag sensors that provide better resolution to analysts about animal fate (Boulêtreau et al. 2018) and manual methods for determining fates from tracking studies (Runde et al. 2021; Fig. 2). These tools and new ones in the future have great potential to expand both applied and fundamental avenues of field research of predator–prey dynamics; however, as discussed there are pitfalls of using telemetry study designs for ascertaining fates and investigating predator–prey dynamics in the field.

Predation is often a relevant component of natural mortality in an applied context to determine how ecosystems should be managed. Threatened populations may experience high mortality rates and predators are often blamed, which can be tested directly using tools to estimate predation rates of tagged animals. Indeed, people are often in conflict with predators (Lennox et al. 2018) and therefore predation rates are important to quantify in the field to estimate the impact of predators on their prey (Pooley et al. 2017). However, analysts must consider whether predation is compensatory or additive if conclusions are to be drawn about the role of predation in prey population dynamics (Sandercock et al. 2011). This may require considerations of where, when and which predators are consuming prey, which can be resolved by tagging. Confident attribution of predator identity may be challenging using many of the methods described herein, which has important implications. In some cases, misidentification of predators could drive false narratives about predators and caution should be exercised when attributing predators of tagged prey without validations.

Predation has always been a reality of studying animals in the wild, including electronic tagging studies in which instrumented animals have been killed by predators (Gallagher et al. 2021). These opportunistic observations of predation have in some cases contributed to advancing our understanding of predation, but now there are specific tags calibrated for the purpose of identifying predation that allow direct testing of hypotheses related to predator–prey interactions (Lennox et al. 2021a). Investigators seeking to design experiments that test hypotheses about predation should consider the welfare implications of such research and design experiments in a way that minimizes the risk of compromising the tagged animals and biasing predation. Methodological studies on this are needed, including laboratory and field tests of anaesthetic withdrawal, risk

perception, flight initiation and maximum speed/endurance following handling and tagging operations. Whether predators can hear or see tags, biasing selection, is also important to consider and further study (Wargo Rub and Sandford 2020). Continued refinement of the tools available and methods testing of various approaches will help this method become an increasingly important component of the ecologist's toolbox for studying predation.

Transparent peer review

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Data availability statement

No data were presented and none are available

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