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Tracking individual animals can reveal the mechanisms of species loss

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Abstract:

As biodiversity loss continues, targeted conservation interventions are increasingly necessary. Stemming species loss requires mechanistic understanding of the processes governing population dynamics. However, this information is unavailable for the majority of animals because it requires data that are difficult to collect using traditional methods. Advances in animal tracking technology have generated an avalanche of high-resolution observations for a growing list of species around the globe. To date, most research using these data has focused on questions about animal behavior, with less emphasis on population processes. We argue that tracking data are uniquely poised to bring powerful new insights to the urgent, global problem of halting species extinctions by revealing when, where, how, and why populations are changing.

The need to understand species' vital rates

As the global loss of biodiversity accelerates [1], identifying the drivers of species loss is essential to preventing future extinctions. Doing so requires understanding the dynamics of **population abundances** (see Glossary) which arise via the gain of individual animals through births (**fecundity**) and **immigration** and losses through deaths (**mortality**) and **emigration** (hereafter '**vital rates**'; Figure 1). Each vital rate can be influenced by biotic and abiotic factors, such as age and conspecific density, or anthropogenic effects, including climate and land use change. Thus, elucidating what factors drive population trends requires disentangling each of the component parts. However, this information is unavailable for the vast majority of species, meaning we are missing critical insight into the threats they face [2]. Indeed, mechanistic insight into the factors that regulate populations remains a fundamental question for ecology [3].

Disaggregating changes in population abundance into component vital rates requires repeated observations of individual animals whose identities are known. Current methods typically rely on resighting or recapturing "marked" individual animals by exploiting distinctive, natural markings or vocal identifiers (e.g., coat patterns, songs) or outfitting them with artificial tags (e.g., leg bands, neck collars, flipper tags). These techniques are extraordinarily time and labor intensive leaving most species sparsely studied. Further, many studies produce estimates which are temporally coarse (often monthly or annual), and inference about vital rates can be based on only one or two observations of each animal. The inherent low temporal resolution of current approaches combined with the fact that many taxa, such as migrant or pelagic species, move over distances far exceeding the bounds of most studies means that many critical demographic processes are missed simply because they are not observed.

Unfortunately, these gaps are unlikely to be filled by the recent proliferation of biodiversity data. Participatory science initiatives (e.g., eBird or iNaturalist) generate enormous volumes of valuable data but do not identify individual animals and, therefore, cannot disentangle vital rates. Camera traps and audio sensors are capable of distinguishing individuals in some cases, but suffer from similar limitations as traditional approaches because they are limited in spatial scope and therefore often cannot pinpoint the extrinsic drivers of vital rates.

Advances in **animal tracking** technology have generated an avalanche of high-resolution location data for a growing list of species around the globe, increasingly without the need to recapture **tagged animals**. A large body of research has focused on the animal movement processes documented by tracking data, generating insights into animal behavior and ecophysiology as well as ecosystem functions [4]. By offering repeated observations of individual animals at an unprecedented scale, animal tracking data could be used to estimate vital rates, but have yet to be widely used for this purpose. Animal tracking systems vary in terms of spatial resolution, fix rate, deployment duration, and data retrieval methods - each affecting the types and quality of inference that can be accomplished (Box 1). Here, we argue that tracking data are uniquely poised to bring powerful new insights to the urgent, global problem of halting species extinctions by revealing new details about when, where, how, and why populations are changing.

Estimating vital rates with animal tracking

Although tracking data may appear to differ from the type of data typically used for understanding vital rates, at the most basic level all animal tracking systems produce repeated observations of marked individual animals and are therefore highly compatible with existing methods (Figure 1) [5]. Tracking data are particularly well-suited to estimating immigration and emigration rates, which are movement-based processes, and have been widely used to do so [5–7]. It is worth noting, though, that a complete picture of sub-population structure, including among-population connectivity may require extensive sampling efforts that are still difficult to achieve. Estimating **survival** from tracking data is becoming more common (e.g., songbird survival during migration or fisheries stock assessments [8–10] ; Box 1, Figure 2), though it remains difficult in many scenarios. Some tracking systems (e.g., collars commonly deployed on large ungulates or some pop-up satellite archival tags) may even support the direct identification of mortality events without recapture and are, thus, able to investigate proximate causes of mortality [11]. Such analyses may allow researchers to disentangle the contribution of anthropogenic activities to mortality from natural sources such as, for example, disease, senescence, or predation (e.g., [12]). Although less well-established, several emerging methods are even beginning to estimate the occurrence of reproductive attempts directly from tracking data (e.g., nesting attempts in eagles [13] and waterfowl [14]) or from **auxiliary sensors** such as vaginal implant tags (e.g., parturition in ungulates [15] and sharks [16]).

Linking tracking-derived vital rate estimates back to changes in population abundance is possible using well-established population demographic approaches [17]. Population models estimate the relative influence of component vital rates on changes in overall abundance by linking these processes via a balance equation (Figure 1) [18]. Integrated population models (IPMs), in particular, are a powerful framework for parsing the influence of vital rates on population change, allowing researchers to integrate disparate data types and link individual-scale data with population-scale monitoring efforts [19,20]. Thus, data from tagged animals can be deployed alongside data from traditionally marked or even unmarked animals to augment existing frameworks. For example, Horne et al. [17] paired GPS tracking data with abundance counts in an IPM to understand the drivers of population dynamics in Gray Wolves (*Canis lupus*).

By allowing data collection to follow individual animals as they move through the environment, tracking data can present key advantages over data typically applied to vital rate estimation, though not without limitations. As tag technology improves, animals are increasingly being tracked for longer durations, sometimes even covering entire lifetimes [21]. However, most tags can still only be deployed for short durations, limiting inference about key processes such as senescence or ontogenetic shifts in vital rates. Still, short duration deployments can produce useful insights over limited time periods or within specific geographic areas of interest. Therefore, depending on the technology used, tracking data can be used to estimate differences in vital rates with greater temporal resolution (e.g., seasonally [22,23]). Many tracking systems offer continental or even global coverage, allowing researchers to observe individuals without regard to study area boundaries and, thus, generate vital rate estimates with high spatio-temporal specificity – even for species that have been traditionally challenging to study, such as small-bodied migratory birds [24] or fish [25]. While many tracking devices still remain too heavy to deploy on smaller taxa [4], impressive progress is being made with tag miniaturization [26], rapidly widening the pool of potential study species (recently extending to radio tracking of individual moths [26]), although a lower size limit will eventually be reached. Expanded network coverage of continental- or global-scale tracking systems (such as Motus [27], ICARUS [28], or several acoustic telemetry networks [29,30]) will help close taxonomic and geographic gaps in vital rate estimation for understudied species.

Modern tracking systems not only generate improved data to tackle questions about population declines, but do so at an unprecedented scale. By largely removing human observation from the data collection process, these cutting-edge methods are able to generate several orders of magnitude more observations per individual animal than traditional approaches. For example, in the time since Movebank, a popular global tracking data repository, launched in 2007 it has registered nearly 300 million locations for North American birds alone (of over 6 billion locations for all taxa worldwide) [31]. By comparison, one of the most comprehensive mark-recapture programs, the North American Bird Banding Program, covering the same geographic extent, has cataloged just over 1.6 million resightings in the same time period [32]. While the higher volume of tracking data may be somewhat redundant for estimating vital rates at, for example, annual scales, it can improve the precision of estimates and, importantly, vital rate estimates at finer temporal resolutions (e.g., seasonal rather than annual survival).

Revealing complex drivers

Decomposing changes in population abundance into component vital rates alone is insufficient to understand the causes of species declines. Instead, doing so requires identifying the factors that drive changes in each of the four component vital rates. This is challenging with traditional approaches because the coarseness of vital rate estimates is unlikely to match highly dynamic environmental and anthropogenic pressures. However, by providing high resolution information on individual animals' locations that can be combined with remotely-sensed information, tracking data can reveal how external drivers influence demographic outcomes, and ultimately population declines [11,22].

Furthermore, animal-borne auxiliary sensors (such as heart-rate monitors or tri-axial accelerometers), present an emerging frontier, allowing researchers to associate animals' movements with non-movement behaviors [33] or physiology [34,35], or even directly measure environmental conditions [36] (Figure 2). Integrating these data streams is already proving useful in linking organismal processes with extrinsic environmental context (e.g. [37]) and could reveal the potentially complex causal pathways through which environmental conditions affect vital rates. For example, using tracking techniques, researchers have recently linked animal mortalities to social context [38], anthropogenic impacts [11], and phenology [39].

Identifying the causes of population declines can be highly complex, as changes in population abundance in one region may, in fact, be the consequence of pressures that highly mobile animals face in disparate regions, such as another continent or ocean basin [40,41]. These so-called "**seasonal interactions**" or "**carry-over effects**" arise when component vital rates vary as a function of previously-experienced conditions [42,43]. Recent work has demonstrated that seasonal interactions may play a large role in driving vital rates [44,45] with cascading effects on population growth [46] and range extent [47]. For example, changes in population abundance of several species of sea turtles assessed at terrestrial breeding colonies arise from vital rate fluctuations during pelagic life history phases in the open ocean [48]. Similarly, population trends in migratory birds have been shown to vary according to flyway, suggesting survival may vary with non-breeding location or migration route [49,50]. Identifying these phenomena is extremely difficult without repeated observations of individuals, so some studies have undertaken the challenging, labor-intensive process of comprehensively investigating multiple populations that are demographically linked [51].

The high-frequency time series generated by tracking devices are increasingly allowing researchers to identify seasonal interactions and carry-over effects, and to do so at the scale of individual animals [52–54]. By looking back across tracking data for past exposure to environmental or anthropogenic factors, researchers can reveal the complex time dynamics governing population abundance (Figure 1). Such analyses may be especially important for identifying demographic outcomes relating to chronic or lagged exposure to climate, resource scarcity, toxins, or stressful environments (e.g., [55]). The fine spatiotemporal resolution of modern tracking data holds the promise of identifying critical periods of the annual cycle as well as key locations with disproportionate influence on population dynamics.

Realizing the potential

Supporting global action to halt extinctions will require generalizing insights across species, locations, and ecological and anthropogenic contexts. Even without further data collection, the current set of tracking data holds tremendous potential to support comparative approaches that include multiple taxa or cover broad spatial extents. Already, synthetic studies that aggregate tracking data from multiple sources are providing critical insights into the ways that humans influence wildlife [56–60]. Efforts to improve sharing [61] and discovery [62] of tracking data, as well as to collate standardized metadata providing detailed individual life histories [63], will help move the field towards quantitatively linking individual responses to drivers of population declines.

While animal tracking can reduce the amount of field effort relative to traditional mark-recapture approaches, deploying tags on animals can still be expensive and labor intensive. Many tracking systems remain prohibitively expensive for widespread adoption. Similarly, safely and ethically affixing devices to animals requires specialized training and, even still, may have negative effects on tagged individuals (e.g., [64]). Efforts to build less expensive tracking systems and expand open-source training opportunities could facilitate greater adoption of these techniques, especially amongst researchers from lower-income countries. Increased data sharing could alleviate the burden on researchers and reduce the risk of unintended negative impacts on wild animals.

In addition to large-scale synthetic studies, targeted sampling of particularly vulnerable or data deficient species can generate key insights that support urgently needed conservation and management actions. One example of such an effort is the Road to Recovery Project (r2rbirds.org) which leverages animal tracking to identify the specific drivers of population declines among the most at-risk species of North American birds. Similarly, the Ocean Tracking Network (https://oceantrackingnetwork.org/) has successfully integrated acoustic telemetry-derived insights into management planning for multiple harvested species [65]. Similar efforts focusing on other vulnerable taxonomic groups or undersampled geographies could contribute essential insights to address declines in populations of some of the planet's most critically endangered species.

Moving forward, continued methodological development will support better vital rate estimation from existing tracking systems. Estimating fecundity from tracking data is not yet widely viable for most species. However, linking tracking data to auxiliary vaginal implant tags allows researchers to infer reproductive attempts or even success for a limited subset of mammals [15] and acoustic or video monitoring, paired with knowledge of species-specific life history, could expand the capacity to do so even further. In general, estimating survival rates from tracking is easiest for large-bodied species that can carry tags with **remote data upload** capabilities (i.e., circumventing the need for recapture). Sampling smaller-bodied species could leverage

automated telemetry or **acoustic telemetry** approaches which use networks of fixed receiver stations and often support much smaller tags (Box 1). New analytical approaches custom-made for these systems promise to expand taxonomic coverage by enabling estimation of survival, emigration, and immigration. However, more work is needed in this area, especially the development of techniques that might be able to estimate reproductive success and productivity.

As we rethink the role that animal tracking can play in understanding population declines, we strongly recommend that new tracking systems are designed for this purpose. For example, sacrificing temporal resolution in exchange for further tag miniaturization and extended battery life could extend taxonomic coverage to the dozens of species of migratory birds experiencing unexplained and dramatic declines in abundance [66]. In the marine realm, increasing tag deployment longevity would improve taxonomic coverage and potential to identify carry-over effects. Further, animal-borne auxiliary sensors that are capable of directly identifying mortality events will prevent confusing deaths with tag loss or malfunction, and location information could be used to confirm status and perform necropsies to infer causality [67]. Already, real-time automated analyses of tracking data, and resulting mortality alerts to (community) scientists, provide opportunities for direct post-mortem analyses of the causes of death of individuals [61]. Finally, pairing location tracking with auxiliary sensors that can record, for example, body temperature or heart rate would allow deeper understanding of the physiological processes associated with variance in vital rates.

Concluding remarks

We strongly encourage the animal movement, population ecology, conservation biology, and biodiversity communities to intensify efforts leveraging the animal tracking data revolution to improve our understanding of the causes of species declines. Such efforts will require dedicated technological advances in tracking hardware, targeted development of new analytical approaches, and increased collaboration and data sharing (see Outstanding Questions). Appropriately leveraging the data on individual animals will provide unprecedented insights into the drivers of population declines and help support more targeted, effective conservation actions.

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Glossary:

- **Acoustic telemetry:** Audio-based system that automatically records detections of tagged animals (typically aquatic) within a fixed sensor array.
- **Animal tracking:** Repeated observations of an individual animal collected by a (typically) electronic device affixed to the animal that records, at minimum, the location and time of each observation.
- **Automated telemetry:** Radio-based system that automatically records detections of tagged animals (typically terrestrial) within a fixed sensor array.
- **Auxiliary sensor:** A sensor, integrated with a basic animal tracking device, that records information about the individual's physiology or environment.
- **Carry-over effects:** At the *individual* level, non-fatal effects, such as poor physical condition or delayed phenology that are carried over from one season to the next to influence vital rates such as reproductive success or survival.
- **Emigration:** The rate at which individuals are lost from a population by moving to a new location (one of the four component vital rates).
- **Fecundity:** The rate at which individuals are added to a population via the production of young that survive to adulthood (one of the four component vital rates).
- **Fix rate:** The frequency with which an animal's position is recorded by an animal tracking device. This can be at regular, predetermined intervals for systems such as GPS, or irregular for systems such as automated or acoustic telemetry.
- **Immigration:** The rate at which individuals are added to a population via movement from another location (one of the four component vital rates).

- **Mortality:** The rate at which individuals in a population are expected to die over some time period (the inverse of survival and one of the four component vital rates).
- **Population:** A collection of individuals with a shared gene pool. Populations can refer to an entire species or some geographically restricted subset.
- **Population abundance:** The total number of individuals in a population.
- **Population growth:** The rate at which population abundance changes, where positive growth implies increasing abundance and negative growth implies decreasing abundance.
- **Remote data upload:** The capability of some tags to collect data onboard and subsequently transmit those data to researchers without requiring recapture.
- **Seasonal interaction:** Events occurring during one period which continue to influence individuals and populations (through density-dependence mechanisms) during subsequent periods, profoundly influencing both ecological and evolutionary processes.
- **Survival:** The rate at which individuals in a population are expected to survive over some time period (the inverse of mortality and one of the four component vital rates).
- **Tag/tracking device:** A device which can be affixed on an individual animal which supports the measurement of, at minimum, time and location data either onboard or by some external system.
- **Tagged animal:** An individual outfitted with an animal tracking device that may or may not include auxiliary sensors.
- **Vital rates:** The four basic processes which can lead to changes in population abundance: fecundity, immigration, mortality, emigration.

<u>Box 1</u>

Study design considerations for estimating vital rates

The design of studies to estimate one or more vital rates will depend greatly on the tracking technology deployed, the particular vital rate of interest, and idiosyncrasies relating to the study system and aims. Some studies may be relatively straightforward to implement whereas others are not yet possible, still requiring technological and/or methodological advances. Below, we briefly highlight major study design considerations, analytical approaches, and opportunities for methodological advances. We do so for three major categories of tracking technology:

Direct position telemetry

This category of tracking technology includes systems where the tag records animal positions (typically using GPS) on-board and transmits those data to researchers, obviating the need for subsequent captures. Many terrestrial platforms transmit data at regular intervals whereas many marine applications require pop-up tags which archive data during collection and then transmit the full dataset as a single bundle at the end of a deployment. The fix rate, precision, and deployment duration of this category is highly variable and highly contingent on idiosyncrasies associated with geographic region, taxa, and biome. While largely restricted to large, terrestrial species, this category is ideal for vital rate estimation because it largely eliminates problematic sample bias arising from detection processes associated with archival or reverse positioning systems (see below and Table 1).

Direct position archival

This category is similar to *Direct position telemetry* in terms of the types of data that can be collected. However, instead of transmitting to researchers, data are stored onboard, requiring subsequent recapture for retrieval. The smaller batteries afforded by the lack of telemetry allow for much smaller tag designs that can be applied to a wider range of taxa and ecological contexts. For example, archival tags offer substantially longer tracking durations than most pop-up tags for marine species that can be recaptured (e.g., [45]). Similarly, lightweight archival tags are increasingly used to track small birds with GPS [68] or light-level geolocation [69]. The need to recapture individuals for data acquisition presents a substantial challenge for study design (Table 1).

It should be noted that there are tag designs which are intermediate between telemetry and archival which have limited capacity to upload. These tags frequently include VHF or UHF transmission of data to automated or manually operated receiver stations. Because of the potentially biased data collection capacity (restricted only to animals that survive and can be recaptured), these tags are more similar to archival in terms of utility for vital rate estimation.

Reverse positioning

Reverse positioning systems rely on a distributed array of sensors that receive signals emitted from tags (typically a radio or acoustic pulse) and determine its location via time-to-arrival or triangulation. Because an animal's location is determined by the network, rather than onboard the tag, these tags are often very light weight and do not require subsequent recapture or telemetry for data acquisition. With respect to vital rate estimation, these systems combine desirable qualities of both direct position telemetry (e.g., no need for recapture) and direct position archival (e.g., small, durable tags) systems. However, the spatial layout and coverage extent of the sensor array remains an open challenge for the field (Table I). Similarly, coupling reverse positioning tags with auxiliary sensors is not normally possible.

Table I. Study design considerations for estimating vital rates from animal tracking.

Category	Example Tracking System	Sampling design	Considerations for estimating vital rates			Examples
			Survival	**Fecundity**	**Immigration/Emigration**	
Direct position telemetry	GPS-Satellite, GPS-GSM, ICARUS, Argos, Pop-up satellite archival	● Tags tend to be large and best suited to relatively large species [4]. ● Tag costs can hinder large sample sizes, especially for designs requiring large spatial coverage (e.g., immigration).	● Direct detection via mortality sensor in large taxa and emerging methods to estimate mortality from position data only [70]. ● May require fewer tagged animals than other methods because the observation process does not need to be modeled. ● Pop-up survival tags, common in marine settings, can infer mortality from depth profiles but provide coarse spatial information over limited tracking durations.	● Direct detection via auxiliary sensors (e.g., vaginal implants). ● Emerging methods to detect as a latent state from position data [13,14] or via movement recursion analyses [71].	● Ideal for estimating movement processes due to wide coverage (often global). ● May require tracking many individuals to adequately estimate this population-level process.	● Prugh et al. [72] paired mortality sensors with GPS tracking to understand interactive causes of mortality in mesopredators. ● Buechley et al. used satellite tracking to assess season-specific mortality rates (particularly during migration) [22].
Direct position archival	GPS, Light-level/Pressure Geolocator	● Tags are often cheaper and lighter than similar direct position telemetry tags, increasing taxonomic applicability and potential sample sizes. ● Large sample sizes can require substantial field-based effort to recapture tagged	● Limited capacity - identical to passive banding/tagging schemes. ● Tracking data restricted to recaptured individuals and thus perfectly confounded with the survival process.	● Detection similar to direct position telemetry but with sample bias arising from the need to recapture individuals. ● Tracking data can inform fecundity estimation when paired with traditional methods to study reproduction.	● Emigration can only be jointly inferred with survival (as with traditional mark-recapture) because data are only recovered from recaptured individuals. ● Immigration is conceptually possible, but would require very large	● Beltran et al. [45] link marine archival tracking to reproductive success.

		animals.			samples.	
Reverse positioning	Acoustic telemetry, automated telemetry, PIT (Passive Integrated Transponders) tag, Internet of Things (IoT)	● Generally the lightest and least expensive option, permitting the largest sample sizes and taxonomic breadth. ● Careful consideration of existing sensor arrays is needed to ensure the entire study area is sampled. ● Researchers can often deploy new sensors to the array which is particularly beneficial for local-scale studies.	● Could be estimated using mark-recapture methods, but typically require large sample sizes [5,73,74]. ● Irregular arrays may present challenges because availability for detection is confounded with location. ● High potential to increase survival inference for marine species currently restricted to pop-up tags or small-bodied terrestrial species currently restricted to archival tags.	● No known methods without linking to auxiliary sensors capable of remote data download. ● Conceptually possible if movement data are sufficiently high resolution (both spatial and temporal) using methods from Overton et al [14] or Eisaguirre et al [13].	● Suitable for estimating movements between populations, given adequate coverage by array(s) [75,76]. ● Restricted coverage and array layout may bias inference.	● Crossin et al. [10] review the use of acoustic telemetry to inform fisheries management, including stock assessments.

Figures

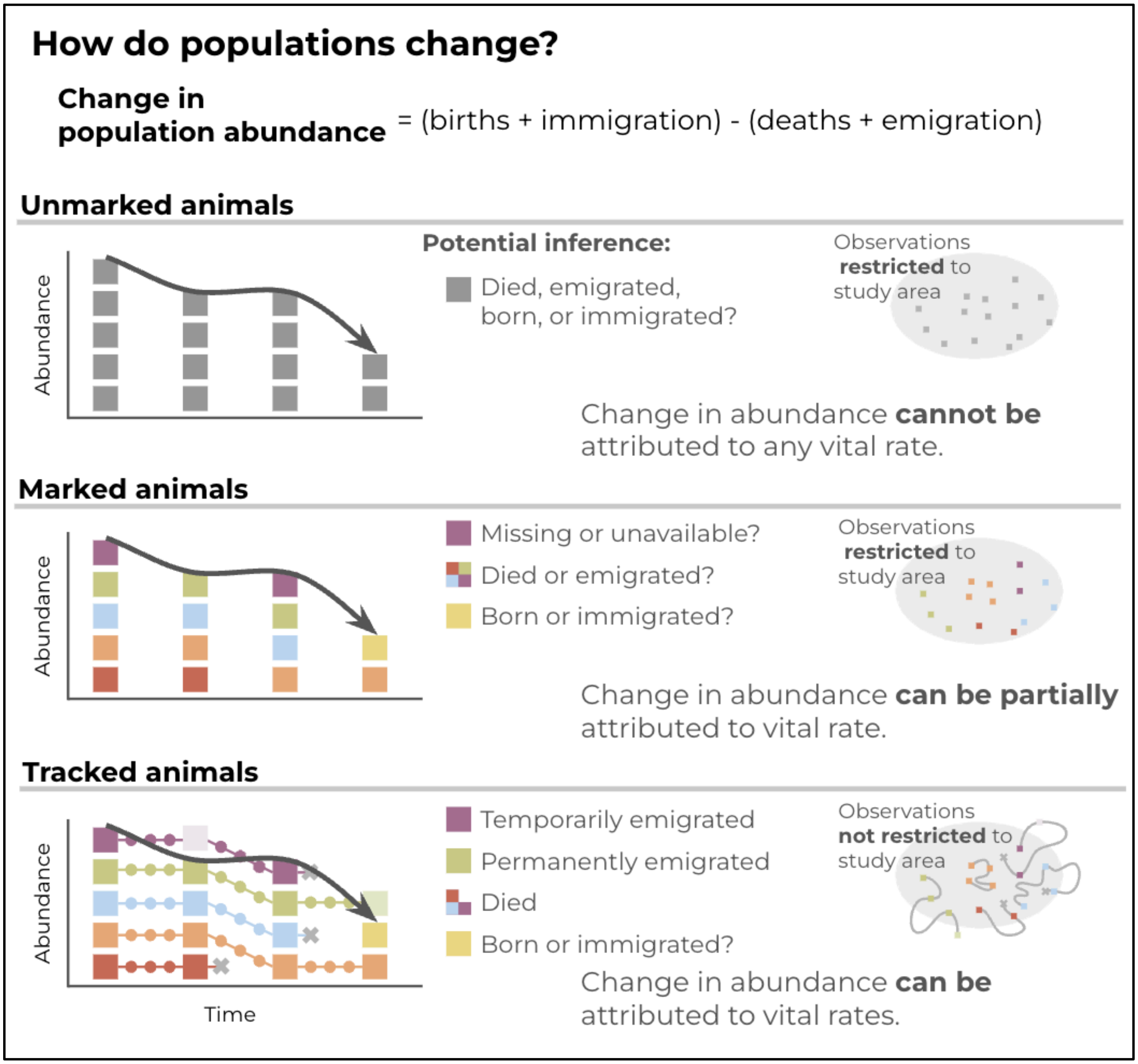

Figure 1. Animal tracking data provides unprecedented detail to how and why populations change. Population dynamics emerge from the four component vital rates, linked via a balance equation: Births and immigrations add to populations, whereas deaths and emigrations subtract from them. Monitoring schemes that do not track individual identities (i.e., animals are "unmarked") cannot estimate vital rates because changes in abundance are confounded. Classic approaches to decomposing vital rates rely on "marked" animal schemes

wherein the identity of individuals are known. These frameworks can partially distinguish vital rates, but because immigration and emigration cannot be fully observed, vital rates cannot be completely disentangled. Most animal tracking, by virtue of finer spatiotemporal resolution and dramatically wider coverage extent, can further decompose vital rates - specifically immigration and emigration processes are better estimated (though births remain an open challenge for the field). Using integrated population modeling, submodels estimating component vital rates can be combined via the overall balance equation and allow researchers to link disparate data types across submodels.

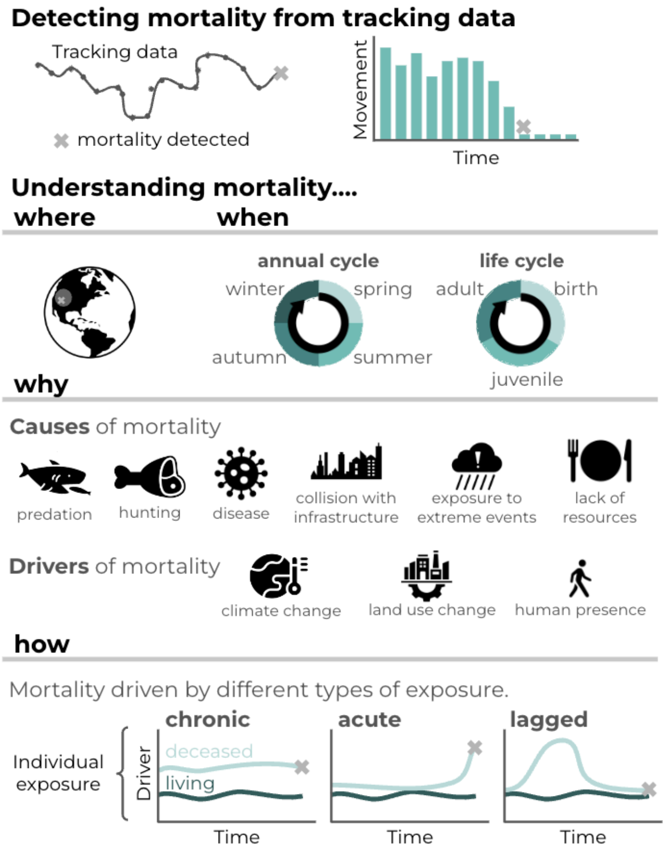

Figure 2. Detecting mortality from tracking data. Using high-resolution GPS data, mortalities can be directly estimated from movement data, pinpointing the location and timing of mortalities. Potential causes can be identified by associating mortalities (and preceding tracks) with environmental variables derived from, for example, remotely-sensed products. Leveraging time series can reveal complex temporal dynamics between drivers and outcomes such as carryover effects and seasonal interactions or chronic exposures.