

Longitudinal demographic data collection

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5.1 Introduction: long-term field studies

Demographic data can be collected during a single visit, or multiple visits, to the population. For instance, a single visit to the field might be in principle enough to collect data on tree rings or fish otoliths, which can then be used to estimate key demographic parameters retrospectively (see Chapter 4). Alternatively, longitudinal studies involve numerous visits to the study population with repeated observations/measurements; this kind of approach typically occurs over multiple weeks, months, years, or even decades, depending on the generation time of the study species, research aims, and available support for the research programme. The collected longitudinal data are then used to estimate demographic parameters such as annual population abundances (see Chapter 7) and/or survival, growth, and reproductive rates (see Chapter 13).

Many long-term studies are running worldwide. In Antarctica, South America, and Central America, the monitoring of avian and mammalian populations has already reached over 50 years in some areas (see [Taig-Johnston et al. 2017](#) for a review). In the northern hemisphere, some of the longest studies even reach 70 years ([Clutton-Brock and Sheldon 2010](#)). Even if there has been a strong focus on birds and mammals ([Festa-Bianchet 2017](#); [Kappeler et al. 2017](#) for some reviews on mammals; [Smith et al. 2017](#); see e.g. [Marshall et al. 2018](#)), long-term studies also exist for other taxa within the animal kingdom (e.g. corals, see [Connell et al. 1997](#); amphibians, see [Cayuela et al. 2020](#)). Long-term field studies are not restricted to animals: long-term plant studies span over 20 years in regions of North America (e.g. [Ellis et al. 2012](#)),

Central America (e.g. [Condit et al. 2017](#)), and Europe (e.g. [Hutchings 2010](#)). Longitudinal data have been, and continue to, be collected on many taxa across the Tree of Life and have provided significant insights in ecology, evolution, and demography ([Clutton-Brock and Sheldon 2010](#); [Reinke et al. 2019](#)). Importantly, demographic data can be collected at the population level (e.g. time series of population counts) or at the individual level (e.g. monitoring of marked and/or geo-referenced individuals throughout their life).

From demographic data collected at the population level (i.e. time series of population counts) and with appropriate methodological tools to analyse them (see the next chapters), several questions can be addressed. For instance, 'What is the population size trend?', 'What is the population spatial distribution?', 'What are the effects of changes in climate on population size/distribution?', and 'What are the effects of human activities on population size/distribution?'. Finer-scale demographic data can also be recorded. For instance, population size time series can be collected with disaggregation into stage, sex, or morph (e.g. counts of adult females). This information is not recorded at the individual level, but still, it is more useful than total population counts. This better resolution can help in tackling some of the questions outlined below with individual-level data.

While long-term data collected at the population level provide significant insights into the population's dynamics, they usually do not allow a full understanding of the underlying demographic mechanisms causing changes in population distribution and abundance ([Clutton-Brock and Sheldon 2010](#)). Indeed,

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changes in population abundance over time can result from changes in rates of births (reproduction), deaths (survival), emigration, and/or immigration. That lack of mechanistic resolution of population-level data is precisely the major limitation of longitudinal studies at the population rather than individual level.

For instance, climate-induced changes in population abundance can result from the sensitivity of a particular stage class (e.g. a particular age) to climate conditions that will exhibit lower survival or fecundity. In the well-studied Soay sheep (*Ovis aries*) population, Coulson et al. (2001) showed that juvenile survival was particularly sensitive to the North Atlantic Oscillation, a weather phenomenon associated with temperature and rainfall. Similarly, within conifer forests, recruitment and growth were associated with fire (Tepley et al. 2017). Interestingly, going beyond population abundance and exploring the effect of climate and human activities on all vital rates and at all stages can also allow one to detect reduced survival and/or fecundity even if population abundance apparently remains stable. For instance, in an eagle owl (*Bubo bubo*) population, adult survival has dramatically decreased because of electrocution, despite constant population abundance, the decline in survival being balanced through massive immigration (Schaub et al. 2010), which could only be detected because the data were collected at the individual level.

From demographic data collected at the individual level, it is possible to accurately identify the proximate causes of changes in population size/distribution and the underlying demographic mechanisms. Thus, questions such as 'What are the effects of changes in climate on survival/fecundity/immigration/emigration rates?', 'What are the effects of human activities on survival/fecundity/immigration/emigration rates?', 'What are the stage classes the most influenced by changes in climate?', and 'Which stage classes are most influenced by human activities?' can be tackled. Identifying the stages and their vital rates (e.g. survival, fecundity) the most affected by climate changes or human activities is crucial in conservation and management to develop appropriate targeted strategies (see Frederiksen et al. 2014 for a review).

In that respect, longitudinal studies at the individual level are powerful. But as with population-level studies, they suffer from limitations. Indeed, implementing individual-based monitoring is generally costly in terms of money and human resources, oftentimes requiring expensive materials (e.g. GPS collars) and experienced fieldworkers during long

periods of time. Moreover, data collected might be scarce due to low sample sizes and because researchers are reluctant to individually monitor individuals in vulnerable populations. In those cases, it might be advisable to take advantage of both population-level and individual-level data, through, for example, an integrated modelling approach (see Chapter 14).

In this chapter, first we introduce the reader to procedures that can be implemented in the field to collect specific demographic data on mobile species (e.g. birds, mammals), at both the population and individual levels. Second, we present the procedures and the type of demographic data that can be collected on sessile species (e.g. corals, plants) at both levels.

5.2 Collection of longitudinal demographic data on mobile species

5.2.1 Procedures and type of data collected at the population level

The problem of imperfect detection while monitoring populations

Within a mobile species' range, the population dynamics can be rather complex. A fragmented landscape means that individuals from the same population can occupy diverse habitat types in space and time. Determining population range size or abundance therein comes with challenges related to two key aspects: (1) spatial variability within the studied area and (2) individual detectability (Yoccoz et al. 2001). Important errors in quantification of population size and emergent dynamics can be made if individuals are missed when they are present at the site, or misidentified, or when the same individual is counted multiple times (Miller et al. 2011). Imperfect detection depends on species characteristics (e.g. camouflage), spatial and temporal variation (e.g. migration), and survey characteristics (Cressie et al. 2009; Guillera-Arroita 2017) (Figure 5.1). Uncertainties in the survey characteristics depend on the type of monitoring, the study design, and the analysis (Figure 5.1). If the aim of the monitoring is to estimate population abundance, the higher the number of repeated measurements and sample size, the higher the precision will be. Accurate estimates (i.e. precise and unbiased; Williams et al. 2002), repeated over time, enable the inference of the drivers of population dynamics, such as climate and harvest regimes (Thompson et al. 1998; Miller et al. 2011; Guillera-Arroita 2017) (Figure 5.1). Under-

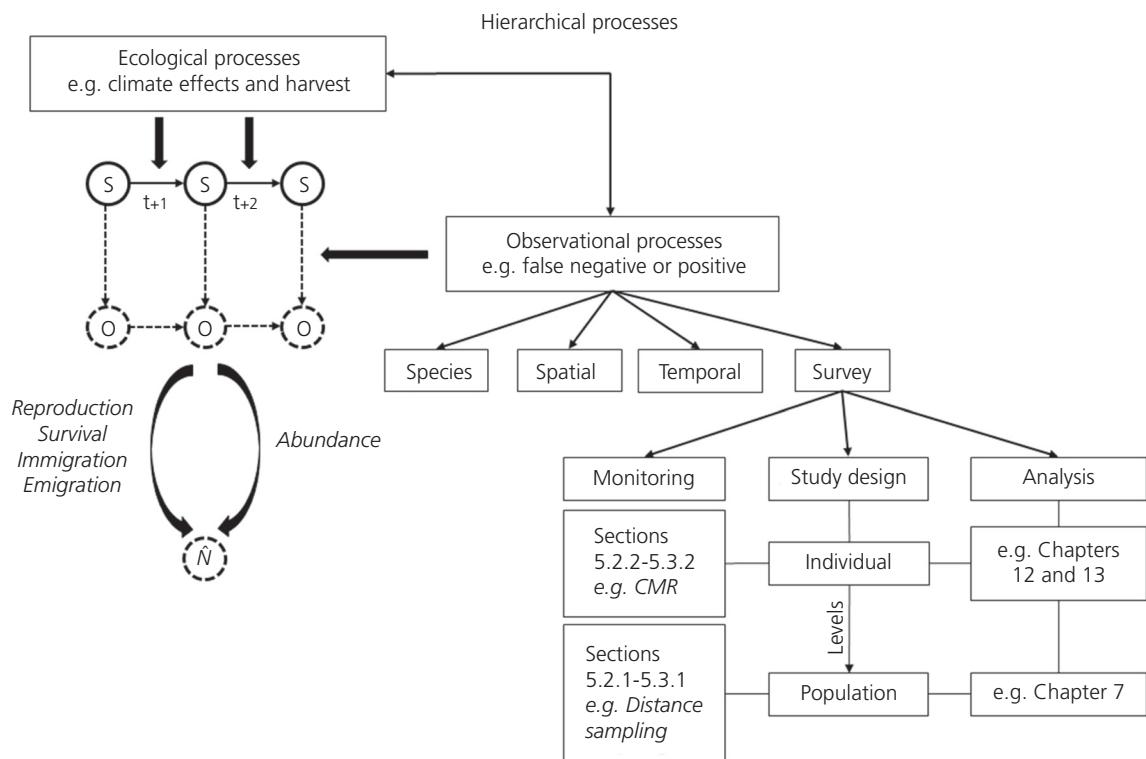


Figure 5.1 Hierarchical organisation of imperfect detection in wildlife systems, inspired from Royle and Dorazio (2008), Zuur et al. (2009), Kéry and Schaub (2012), and Guillera-Arroita (2017). The true abundance is a latent state (S) changing at each time-step, for example year to year (from year $t+1$ to $t+2$), due to changes in vital rates (survival, reproduction, immigration, emigration) affected by ecological processes. At each time-step, monitoring of vital rates or population abundance results in observations (O), such as the observed abundance (\hat{N}). Each of these observations is subject to observational processes, which can be decomposed into distinct components. Population survey is one of the components and consists in applying the required monitoring in the field, using the appropriate study design (at the population or individual level) and then using appropriate analyses to make inferences (modified from Le Moullec (2019)).

over-estimation of abundances or range sizes can have important consequences; for instance, they can lead to ineffective management and incorrect conservation decisions (Sinclair et al. 2006).

A large diversity of methods for monitoring populations

Monitoring populations over years to determine range size and/or abundance has been central in the field of ecology and wildlife management since the 1930s (Krebs 1998; Williams et al. 2002; Sutherland et al. 2013), and a large diversity of methods has emerged since (Seber 1992; Thompson et al. 1998; Sutherland 2006; Morellet et al. 2011; ENETWILD Consortium et al. 2020). The monitoring method chosen by a manager/scientist, the 'tools' (e.g. camera traps, permanent plot) used to increase the overall detectability of

species, as well as the spatial coverage vary according to the species characteristics, including its rarity and detectability in the environment (Figure 5.2). Thereafter, data can be collected with multiple monitoring methods and sampling designs (see Figure 5.2): for instance, camera traps located at random or stratified designs can be used with capture–recapture or distance sampling. Several of the listed monitoring approaches here are also applicable to sessile species (see section 5.3.1).

Estimating population abundance can be performed on an absolute or relative scale with direct or indirect population counts. Absolute abundance methodologies aim to estimate the true population size, that is, the state variable, while relative abundance methodologies (e.g. capture rate, hunting records, sign detection rate, activity indices) estimate the population size relative

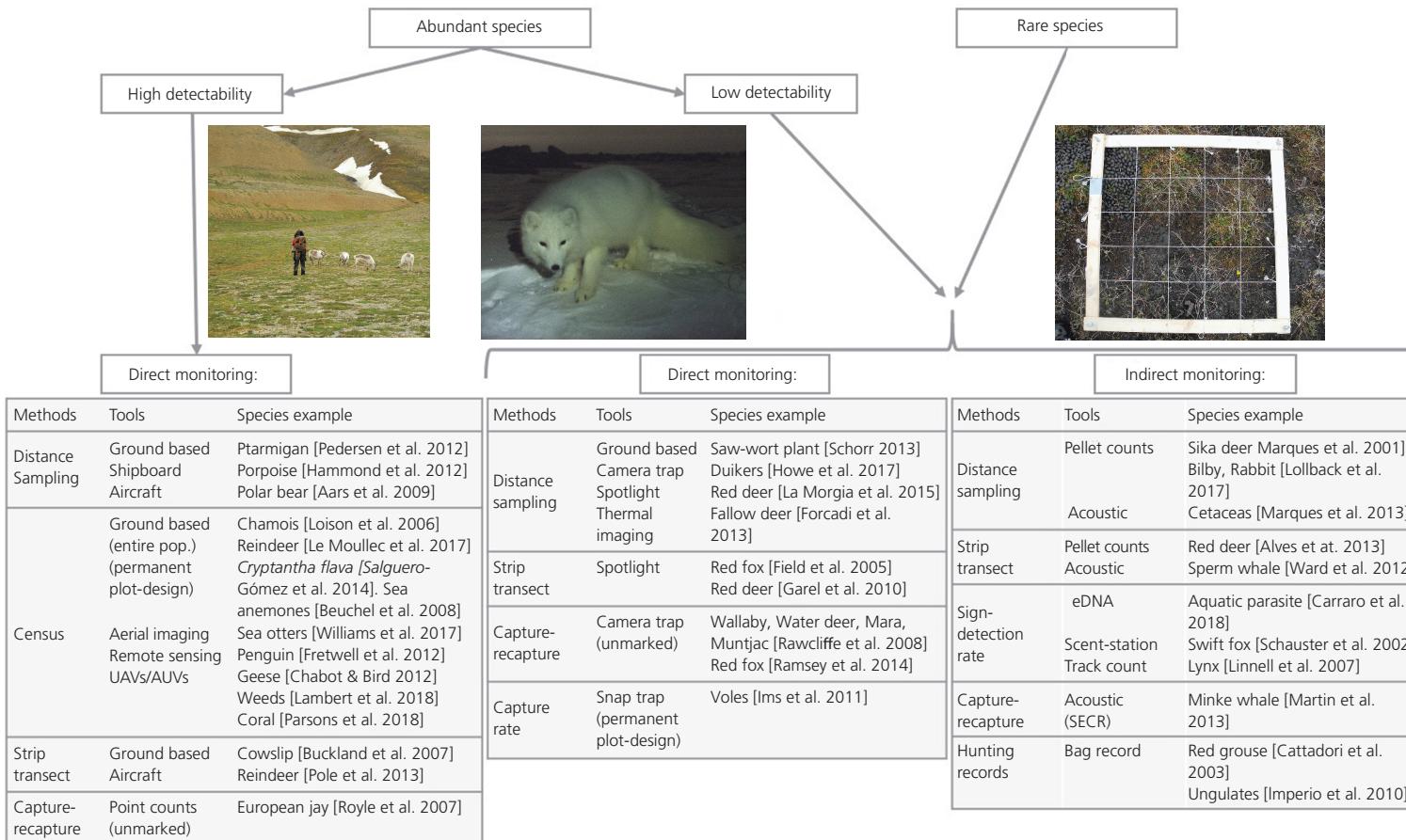


Figure 5.2 Examples of monitoring methods for the estimation of population abundance in animals and plants. A same monitoring method can be conducted with the help of different tools to increase species detectability and spatial coverage. UAVs = unmanned aerial vehicles; AUVs = autonomous underwater vehicles; SECR = spatially explicit capture–recapture (unmarked individuals); eDNA = environmental DNA (credit A. Tholfsen / M. Le Moullec).

to a previous survey (Pollock et al. 2002; Hopkins and Kennedy 2004; O'Brien 2011; Amos et al. 2014). Importantly, the latter approach assumes a constant detection probability and thus requires constant survey design, personnel training, species behaviour, habitat use, and range size between survey events. Under such conditions, the trends in abundance can inform managers' decisions. However, relative estimates of population size cannot be compared across systems (Amos et al. 2014).

Abundance estimates from direct individual counts within a population require visual detection of the organism (i.e. total counts, camera surveys). These methodologies are often preferred (Morellet et al. 2011) and are adapted for abundant, tame, and easily detectable species, since they are 'data hungry' for robust modelling and often logically costly (Yoccoz et al. 2001; Guillera-Arroita 2017) (Figure 5.2). Consequently, these approaches are often restricted to small-scale studies (but see Yuan et al. 2017). Monitoring methods for rare or hard-to-detect species, such as cryptic, nocturnal, forest, or aquatic species, require the use of specific tools to increase detections and spatial coverage (e.g. spotlight, thermal imaging, acoustic recorders) (Marques et al. 2013). For instance, to monitor marine species, unmanned underwater vehicles (UUVs) can be coupled with postproduction computing algorithms to obtain the relevant demographic information (Smale et al. 2012). Notably, the large diversity of existing methods to monitor populations in terrestrial systems is still valid in marine environments (see Katsanevakis et al. 2012 for a review). In some cases, indirect population counts based on signs detection (e.g. fecal pellet counts, track counts, or environmental DNA) can be better suited to the task (Pollock et al. 2002; Thompson 2004; MacKenzie et al. 2005; Jones 2011).

The methodology chosen to study a population should preferably be associated with a measure of detection probability that is inherent to certain methodologies, such as distance sampling (Buckland et al. 2007a), or capture–mark–recapture (Yoccoz et al. 2001). Capture–mark–recapture is further developed in the next section on individual-based methods, yet inferences on population abundance can be drawn from this methodology too. More generally, information on organism resightings (marked or unmarked) (Royle et al. 2013) is often combined with monitoring methodologies to access information on detection probability, that is total counts (Le Moullec et al. 2017), and camera traps (Karanth and Nichols 1998).

Methods for spatially referenced observations

Spatial referencing of individual observations (i.e. coordinates, spatial unit) within a population enables researchers to relate the frequency of detections of individuals to the surrounding conditions, that is spatially referenced environmental covariates (Aarts et al. 2012; Guillera-Arroita 2017). Thereafter, within the modelled spatial distribution of the species, population density can be predicted in areas or periods of time not surveyed, as long as extrapolations are done within the range of data monitored (Sillett et al. 2012). Random sampling of individuals across the study region is fundamental to unbiased design-based studies. However, model-based studies grant access to a large diversity of study designs and opportunistic count data collection. Aarts et al. (2012) demonstrated the similarities in spatial density estimates between count data collected in discrete space (i.e. number of observations per spatial unit) or in continuous space (e.g. use-availability, where each individual is treated as one observation) and presence–absence data (if the spatial unit corresponds to single observations). Hence, data to model the spatial density can be diverse (Baddeley et al. 2006; Zuur et al. 2009; Royle et al. 2013; Ramsey et al. 2015; Williams et al. 2017; Antún et al. 2018; Le Moullec et al. 2019). Spatiotemporal variations in detection probability are often accounted for, prior to analysing the spatial density function (i.e. two-stage approach), but in some cases the detection and density function are estimated simultaneously (i.e. one-stage approach) (Royle et al. 2013).

5.2.2 Individual-level long-term field studies: concepts, methods, and data

Methods that allow individuals within a population to be uniquely recognised have given rise to a plethora of long-term studies of wild animal systems that have been formative in our understanding of their ecology, evolution, and conservation biology. The ability to individually recognise animals has not only provided mechanistic insights into the drivers of the patterns often considered by long-term population-level studies (such as the movements between, and age structures within, populations, and the causes of changes in fitness or selection), but also proven foundational in understanding social structure, individual-level fitness, and the links between different life history stages and generations (Clutton-Brock and Sheldon 2010). This section explores current and developing procedures used to collect data at the individual level

in these long-term studies, the types of data these approaches provide, and the new implications that recent advances are allowing.

Individual-level monitoring using physical captures

The fundamental premise of long-term individual-based field studies in animal populations of mobile species has long been, and continues to be, the individual-level ‘capture, mark, recapture’ (CMR) procedure (see Figure 5.1); an individual is ‘captured’ (physically or simply recorded), ‘marked’ in a uniquely identifiable way (through active intervention or through documenting individually recognisable characteristics, such as marks on the tails of whales; [Pomilla et al. 2014](#)), and ‘recaptured’ (or ‘resighted’) at a later time (i.e. re-recording the unique identity of that individual). The particular protocols employed for each of these stages of the individual-level CMR procedure are specific to the species under consideration and the practicalities of fieldwork. However, following this standard’s underlying logic, these procedures are constantly refined as new techniques and technologies become available and applicable to these valuable long-term study systems.

One of the best examples of the progress of specific protocols comes from the earliest of the long-term individual-based field studies: wild birds, particularly tits (great tits, *Parus major*; and blue tits, *Cyanistes caeruleus*), which started as long-term study populations across Europe in the 1940–1950s ([Kluijver 1951](#); [Lack 1966](#)). These species readily breed in nest boxes during the spring, so individual CMR protocols can quickly be developed. They are based on physically capturing individuals as breeding adults or nestling chicks, marking them with a unique identifier (a metal leg ring with a unique code), and recapturing and identifying them in following breeding seasons. This standard procedure was widely and rapidly adopted across a range of systems (not limited to animals—see below) and remains a common method across various long-term population bird studies ([Grant 1986](#); [Nisbet 1989](#); [O’Connor 1991](#); [Perrins et al. 1991](#)).

Advancing longitudinal methods: progress in individual-level monitoring

Although effective, the nest box ringing procedure meant that these early individual CMR studies within these systems were limited to monitoring individuals at specific locations (e.g. nest boxes) and restricted to particular time-frames (i.e. during breeding). As such, further techniques were soon developed to expand

beyond these restrictions, either using mist-netting to capture, mark, or recapture these birds outside of the breeding period (such as during winter foraging; [Perrins et al. 1991](#)) or using colour bands (displaying unique combinations of rings of colours) to allow non-physical ‘recapture’ via resightings ([Ekman 1989](#)).

The aforementioned initial developments allowed for individual monitoring to be less spatiotemporally restricted than previous protocols. However, the advances with the largest potential for these particular systems (and most of the individual-based long-term study populations generally) have come from recent technological developments in automated animal tracking systems ([Bridge et al. 2011](#); [Kays et al. 2015](#); [Jönsson et al. 2016](#)). For instance, various long-term study populations of tits now tag captured individuals with passive integrated transponders (or PIT tags) that are either contained within plastic leg rings or injected subcutaneously. These PIT tags contain a microchip with a unique identification code that can be read, and automatically recorded (i.e. allowing ‘resightings’), by radio-frequency identification (RFID) stations. The stations can be placed at nest boxes during the breeding period ([Firth and Sheldon 2015](#); [Schlicht et al. 2015](#); [Firth et al. 2018](#)) or at feeding stations to allow large-scale resighting during the nonbreeding season ([Firth and Sheldon 2016](#)).

More generally, RFID technology is emerging as a particularly good example of applying tracking technologies within long-term individual-based study populations. This is because RFID is well suited to these systems due to the size of the tags (often <1 g), their relative affordability, and the lifelong readability of the microchips which do not require an internal battery (as they are passive). As such, marking individuals with unique PIT microchips is now a prevalent and staple method of individual CMR systems, not just for long-term bird studies ([Bonter and Bridge 2011](#)) but also across various populations, ranging from insects to fish to mammals ([Gibbons and Andrews 2004](#); [Rehmeier et al. 2006](#); [Silcox et al. 2011](#)). Remarkably, these new technologies tend to be less invasive. While toe clipping for small mammals has been the rule for a long time in CMR protocols, these new technologies (e.g. camera trapping and noninvasive DNA; see also Chapter 1), now favour noninvasive censusing.

The development of a diverse array of exemplary methods for individual-based monitoring of animals comes from long-term studies of mammalian systems ([Clutton-Brock and Sheldon 2010](#); [Hayes and Schradin 2017](#); [Schradin and Hayes 2017](#)). Indeed, some of the longest and most substantial individual-based

study populations are mammals, partly due to the ease of 'resighting' these animals, especially for island populations of large mammals where immigration/emigration do not exist, and habituation is rapidly achievable due to the lack of predation. For example, long-term studies such as those on red-deer (*Cervus elaphus*), which began in 1971 on the Isle of Rum, Scotland (Clutton-Brock et al. 1982), and Soay sheep, which began in 1985 on St Kilda, Scotland (Clutton-Brock and Pemberton 2004), have been successful in consistently employing standardised protocols based on capturing and uniquely marking individuals shortly after birth, and then resighting these individuals via regular censuses of the study populations thereafter. Mammalian systems in less-convenient settings have benefitted substantially from recent advances in monitoring procedures (Noonan et al. 2015; Hays et al. 2016; Nowacek et al. 2016). For example, bat species hold many of the same conveniences that long-term bird systems allow (i.e. occupying researcher-made boxes, as well as ease of capture in mist nets). As such, these systems were also originally based on monitoring using individually coded rings but are now converging on the same technological approaches found to be useful for monitoring bird systems, for example using PIT tags and RFID technology (Fleischmann et al. 2013; Law 2018) that allow automated resightings instead of relying on physical captures. Similarly, many mammal systems have benefitted from the miniaturisation of GPS technologies providing high precision and constant monitoring (Tomkiewicz et al. 2010; McMahon et al. 2017).

Long-term studies based on species that spend large proportions of their time underground (therefore restricting the use of GPS) have had to consider other approaches. For example, the UK European badger *Meles meles* project, which started over 30 years ago (Macdonald and Newman 2002), was traditionally restricted to overground monitoring or capture/resighting procedures. Now, magneto-inductive tracking techniques are available which allow automated, continuous, fine-scale monitoring of individuals whilst underground (Noonan et al. 2015). These techniques hold much potential for other long-term studies for other ground-dwelling species (Schradin and Hayes 2017).

One of the most important potential applications of technology for longitudinal studies of individual animals in relatively inconvenient settings may well be for studies of marine mammals (Hazen et al. 2012; Mann and Karniski 2017). Here, long-term monitoring has long been based on identification of individuals

in photos gathered from opportunistic sightings or transect surveys (Eguchi 2014; Urian et al. 2015), which makes individual monitoring often very difficult (Mann and Karniski 2017). Advances in a range of tracking technologies, from drone surveys to newly developed animal-borne tags (Hussey et al. 2015; Kays et al. 2015; Nowacek et al. 2016; Hays et al. 2019), will provide ripe opportunity to rapidly advance the monitoring of these systems, by allowing individuals to be monitored over their entire lifetimes.

The new technological monitoring methods also provide the potential for continuously tracking movements at fine scales (e.g. within resident territorial species) as well as over larger distances for migratory species, and even nomadic species moving in irregular manners (Teitelbaum and Mueller 2019). Further, it is becoming possible to integrate technology providing detailed physiological monitoring of individual states, activity, and metabolism into tracking devices (see Chapter 2). Such information is particularly valuable within long-term study systems for which the basic underlying ecology is already well researched, and this now provides the potential to allow vast advances in knowledge surrounding the causes and consequences of individual states (Hayes and Schradin 2017; Schradin and Hayes 2017). Yet, one of the most important additional advantages of large-scale automated methods is that these new approaches allow for simultaneous monitoring of all individuals over large spatiotemporal scales, thus providing unprecedented insight into the social structure of natural populations (Krause et al. 2013; Firth and Sheldon 2016) (see Chapter 3).

5.3 Collection of longitudinal demographic data on sessile species

Sessile species are those that lack the ability of (self-)locomotion. From a life cycle perspective, sessile species typically correspond to species where established life cycle stages are anchored onto a substrate. Naturally, plants adhere to this definition, though some remarkable exceptions in the Plantae kingdom do exist, such as the polytomic group of tumbleweeds (e.g. genus *Kali*, *Amarnathus albus*, *Salsola* spp.) and the Rose of Jericho (*Anastatica hierochuntica*). However, sessility is not unique to plants. Indeed, entire taxonomic groups of the animal kingdom, such as corals and sponges, as well as other species of important economic value (e.g. barnacles), are sessile. In addition, fungi and a significant percentage of bacteria (e.g. Geesey et al. 1978) have sessile modes of life.

The monitoring of sessile species has some advantages over that of mobile species, in that mortality in sessile species cannot be confounded with the individual not being at its previous location due to mobility. As such, the classical equation modelling the changes in population size (N) over time as a function of the rates of births, deaths, emigration, and immigration can be reduced to just two terms, births and deaths, assuming that dispersal (as well as mobility) does not occur. However, modelling the demography of sessile species has its own specific challenges. Indeed, sessile species, because they are 'stuck' in place for most of their life cycles, have evolved strategies to cope with the local environmental conditions (Huey et al. 2002; Svensson and Marshall 2015; Žádníková et al. 2015). It is precisely the strategies of some of those sessile species that causes new challenges for the monitoring of natural populations in sessile species. These strategies include clonality, dispersal, propagule dormancy, vegetative dormancy, creeping, and mimicry, among others, and are discussed below.

5.3.1 Procedures and type of data collected at the population level

Many of the field approaches described above to quantify and estimate the population size, distribution, and structure of mobile species are also relevant to sessile species populations (Figure 5.2). However, field techniques to monitor sessile populations tend to capitalise more on their immobility. Consequently, permanent plots, quadrats, and transects are the standard methods used in sessile longitudinal demographic studies. Nonetheless, technological advances are also reshaping how natural populations of sessile species (e.g. plants and otherwise) are monitored.

The increase in satellite data resolution now means that counts of individuals are achievable in ecosystems where density is low, individuals are distributed at random or quasi-random, and where there is little three-dimensional layering (Bai et al. 2011). Desert and Mediterranean ecosystems, for instance, are ideal candidate systems where these technologies show more promise (Peters and Eve 1995). In contrast, monitoring the population dynamics of sessile species in tropical and marine ecosystems remains more challenging. This is because, in these cases, populations of sessile species tend to have complex elevational structures, where only adults who have broken through the tight canopy (or dense marine reef community) are readily observable with satellites, and thus for which little information is directly available for other stages.

Novel light detection and ranging (LIDAR) technologies can complement data acquisition through their ability to operate in high-density stands (Malhi et al. 2018). In this regard, the application of the approaches discussed regarding the detectability of different life cycle stages in mobile species is just as equally useful here (Figure 5.1). In addition, the development of low-elevation aerial technology holds great promise, though the challenge remains in how to navigate this technology in landscapes full of handicaps, such as rocks, wind/water currents, tree trunks, lianas/algae, and small stems/debris that may not be adequately identified by navigating devices equipped with smart technology (but see <https://www.ox.ac.uk/research/research-impact/poetry-motion>). Some key applications of drone (unmanned aerial vehicle, UAV) technologies have been targeted specifically for agricultural use (Saha et al. 2018; Jiménez López and Mulero-Pázmány 2019). These approaches, coupled with artificial intelligence to automatically distinguish and track individuals (Ampatzidis et al. 2019), represent a unique opportunity to quantify population number and even structure in sessile organisms (Figure 5.3). It is worth mentioning here that the power of these novel technologies cannot be harnessed efficiently without taking into account the pertinent advances in image analysis (e.g. Maillard et al. 2010; Bruijning et al. 2018). The monitoring of sessile populations below water is faced with important challenges due to obvious logistical considerations, such as lack of oxygen, strong currents, and high viscosity. But novel developments from physics now also allow for the treatment of seawater waves as magnifying glasses to evaluate coral reef properties at high resolution using UAVs (Chirayath and Earle 2016).

5.3.2 Procedures and type of data collected at the individual level

While age estimation methods do exist for sessile species (Chapter 4), age estimation in species such as plants, corals, or sponges in a way that is not destructive—and thus compatible with long-term censuses—is challenging. For that reason, among others related to convenience (Ebert 1998), the tracking of individuals in sessile species' populations, as well as their modelling (e.g. Chapters 9 and 10), tend to include information on not only survival and reproduction but also changes in individual size (rather than age) through time. In fact, size is the most widely used

predictor of fitness components in the demography of sessile species (Caswell 2001; Caswell and Salguero-Gómez 2013).

Size in the field can be measured according to different morphometric variables, including but not limited to the diameter at breast height (e.g. in trees), basal diameter (e.g. in shrubs), area (e.g. in corals and sponges), degree of modularity/architecture, and number of stems, and so on (Salguero-Gómez et al. 2015). When deciding which morphometric variable to collect data for, it is key to consider various factors, such as (1) *a priori* knowledge on the biology of the species and its life cycle and (2) the traits that most

inform on the vitality of the individual (e.g. height may be an important trait in light-limiting terrestrial habitats, while area/volume ratio is an important one when considering exposure to the environment). The state predictor can be based on ontogeny, rather than different dimensions of size. Classical categories of ontogeny have been developed for plants (Gatsuk et al. 1980), though these ignore non-progressive life cycles. It is recommended that, if *a priori* knowledge regarding the life cycle of the species does not exist, researchers collect multiple axes of information regarding the structure and ontogeny of the individuals in the first few field seasons and quickly construct and compare vital

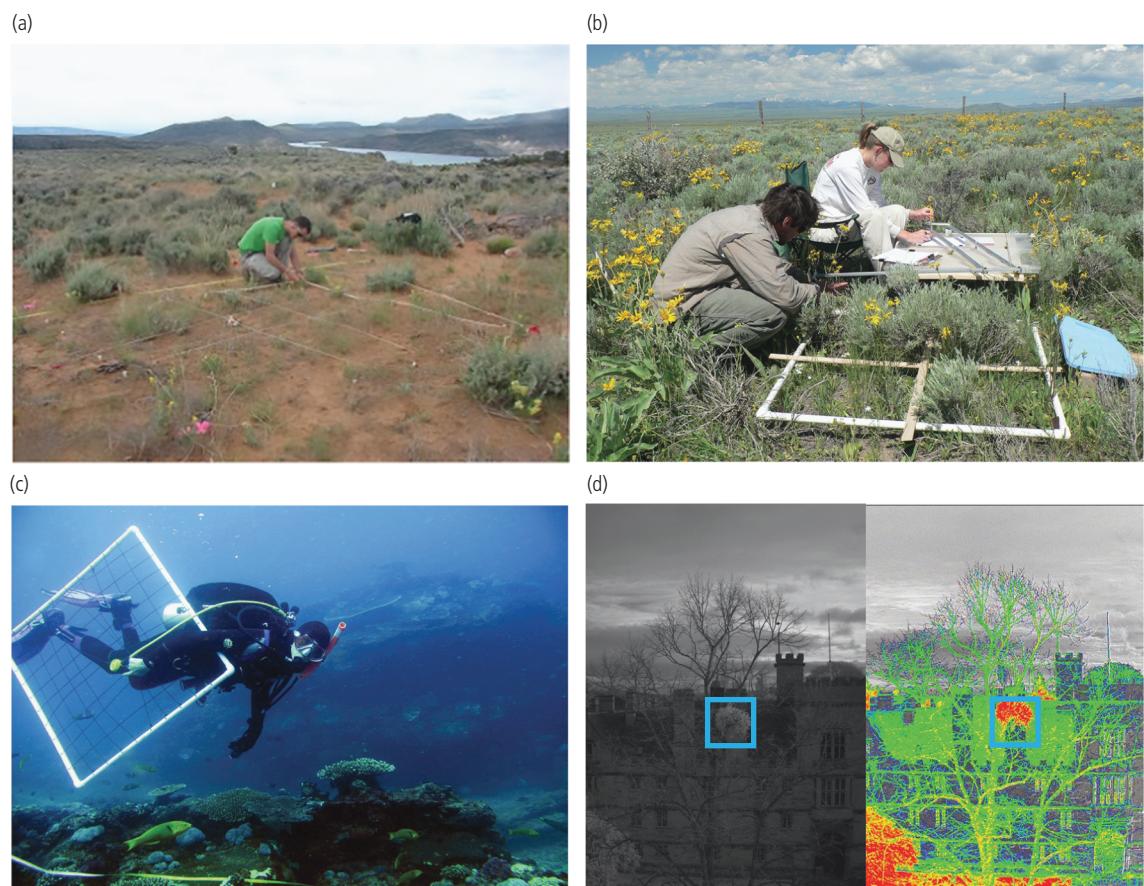


Figure 5.3 Examples of monitoring methods for the estimation of population abundance, density, structure, and vital rates in sessile organisms.
 (a) Permanent plots can be used to quantify and track population dynamics of organisms fixed on a substrate (credit R. Salguero-Gómez).
 (b) A pantograph allows for the spatially explicit depiction of population (and community) structures in a compact, reliable, and fast way (credit P. Adler). (c) Quadrats and transects to track populations/individuals can be used on both terrestrial and aquatic systems (credit M. Beger).
 (d) UAVs, coupled with artificial intelligence algorithms, are starting to allow for the accurate, fast, and convenient measurement of population dynamics of sessile organisms. Photos show the visible range (left) vs. hyperspectral range (right) of a photo containing a parasite (blue square), a mistletoe (credit R. Salguero-Gómez).

rate models to evaluate the best predictors. This information can then help guide a more efficient, fine-tuned (and less-laborious) field monitoring protocol.

The kind of data that need to be collected to examine the population dynamics of sessile species often requires marking or mapping individuals in a way that allows researchers to relocate them in the next site visit. In terrestrial systems, marking/mapping can be done with sticks, coffee stirrers, pin flags, nails, or tags attached to each individual. Each marker needs an unequivocally distinct ID—this can be done through marking each device with pen or by producing tags that have a unique ID system. Another key attribute of these IDs is that they need to ‘survive’ themselves to the next census. Often, and depending on the climate at the study location and the kind of material (and presence of herbivores and people!), tags can go missing, and the researcher must update missing IDs with new tags based on a ‘best guess’ system supported by the GPS coordinates of the surrounding individuals whenever possible. It is recommended that, when analysing the field data (e.g. Chapters 9 and 10), the models should be updated with perfect and retagged individuals to evaluate potential sensitivities of outputs to field assumptions on ID assignment. Nonetheless, since markers can go missing frequently, photography of the study plots for every census is strongly recommended. This photographic evidence can become invaluable when trying to figure out the location of not only individuals but also entire permanent plots located in dynamic ecosystems, such as dunes and marine environments.

There are pros and cons of using tags of different materials: plastic and wooden ones can rapidly degrade, whereas aluminium tags tend to attract the attention of herbivores and vandalism. An additional approach consists of marking the corners of quadrats with metal bars that can be pounded in the soil/rock and whose positions can be relocated every visit with the help of metal detectors. Once the positions of the quadrat (or transect) have been located, the Cartesian coordinates of the individuals should allow researchers to relocate established individuals and identify new recruits. However, it must be noted that sessile individuals, contrary to common belief, do move, if only a little bit. Another important consideration is that metal markers can leak materials into the soil and also affect the temperature of its microclimate (Nassar et al. 2018). Individuals of species’ populations found in high-density, overlapping statures and/or small sizes can prove particularly challenging to mark and relocate. In these cases, we suggest marking/mapping the

locations of individuals in a subset of permanent plots and trying to mark them again a week later using different methods, and then comparing the accuracy and feasibility of each. Certain GPS systems that offer resolution within centimetres are of particular interest here too (Lee and Ge 2006).

Certain sessile organisms with cryptic life stages can pose interesting challenges to monitor the dynamics of their populations. A feasible approach here involves the careful exploration of such stages on the permanent plot in a nondestructive way. For instance, some species undergo dormancy: the aboveground biomass is completely lacking, but organisms are alive below-ground. Dormancy comes in the shape of propagule (e.g. seed) dormancy, vegetative (e.g. established individual) dormancy, and roots. In this realm, nondestructive approaches involve carefully excavating roots or bulbs to determine if the individual is alive (Bierzychudek 1982). An alternative approach here is to make the assumption that if a number of years have elapsed since the last time that the individual was observed aboveground, this individual is declared dead. In this context, prior knowledge about age-based and environmentally driven mortality schedules can be crucial. However, recent Bayesian statistical frameworks inspired in capture–recapture methods can be applied to cope with this uncertainty (Colchero et al. 2012; Paniw et al. 2017).

Clonality is an important challenge in demographic studies. Indeed, the incorporation (or not) of explicit clonal architecture in demographic studies has been a point of contention since the very inception of modern plant population ecology (Harper 1981). The considerations here are important because, although different segments (i.e. ramets) of a clonal individual (i.e. genet) can have a great deal of independence (Hutchings and Price 1993; Vuorisalo and Hutchings 1996), and can even compete against each other (Price et al. 1996), considering them all as separate individuals or parts of the same one will affect how the individual is tagged, how the models are defined and constructed, and ultimately the outputs from such demographic analyses (Janovský et al. 2017; Salguero-Gómez 2018). For instance, data from the same permanent plots where the functional unit *individual* has been established ignoring clonal links (i.e. the researcher tags seemingly independent units that are in fact part of the same genet as separate individuals) will inevitably result in the estimation of higher generation times and more variable population growth rates than if done on the basis of genetics (Janovský et al. 2017).

5.4 The future of long-term studies: new aspects, current biases, and arising challenges

Long-term studies clearly hold a large range of benefits compared to a single visit to the field or compared to short-term field studies. They play a crucial role in our understanding of the drivers of population dynamics and in the assessment of their demographic status (e.g. decline, remain stable, increase in size over time). As such, they are important to inform policy (see Chapter 19) and to answer societally relevant questions (Hughes et al. 2017). It is also needed to consider the potential biases, the aspects still requiring advances, and the potential arising challenges of these systems. For instance, in regard to biases in the systems currently under long-term individual-based monitoring, it is notable that species that are relatively easy to study using traditional CMR techniques are still heavily favoured over ones that it may be difficult to apply these techniques to. Nevertheless, in the dawn of new technologies providing novel avenues of monitoring, it could now well be the case that other species are particularly well suited to new methods despite been previously difficult to monitor with standard approaches. As such, diversifying long-term individual-based studies across the Tree of Life may shed new light on ecology from the viewpoint of currently understudied species and allow previously unrealised potential to be recognised.

One of the most lasting and widely acknowledged challenges of long-term study systems is their ‘mismatch’ with the modern scientific funding structures that often work in short-term research grants designated to proposals aimed at pursuing set hypotheses over relatively short periods of time (often 2–5 years) (Clutton-Brock and Sheldon 2010). This fact, combined with the growing ‘publish-or-perish’ climate across biology and most other scientific disciplines, means that short-term output is often largely favoured over longer-term goals—which can, nonetheless, be better representative of the ecology and evolution of the studied population. As such, the success of individual-based long-term study systems often relies on the continuation of short-term studies taking place within their larger framework (Schradin and Hayes 2017). Thus, it is now important that technological advances be employed to address this challenge, rather than magnify it.

Continuously applying new methods to long-term study systems may allow for their value to be constantly recognised. There are already numerous examples

of successfully applying new monitoring technologies for short substudies within long-term systems (rather than integrating within the whole standard protocol) to address specific hypotheses in new ways, for example using GPS to examine foraging in the long-term Kalahari meerkat (*Suricata suricatta*) project (Gall and Manser 2018). Further, the development of technologies that allow automated manipulation (rather than just monitoring) can provide a platform to carry out individual-level experiments within long-term study systems, for instance applying automated experimental treatments to individuals based on their unique RFID codes in the Wytham tit project (Firth and Sheldon 2015). Clearly, updating long-running systems with the ever-developing new approaches provides many possibilities to acquire continued research funding for these crucially important study systems.

Finally, a more contemporary challenge arising in the new age of monitoring long-term studies is how to most efficiently deal with the vast amounts of data arising from these systems. Automatically recording information for many individuals within these populations over large periods of time at fine-scale resolutions is the dream of any population ecologist, resulting in the production of millions (Firth and Sheldon 2016) or even billions (Noonan et al. 2015) of data points. The analytical techniques developed to handle this scale of data, ranging from simply dealing with the raw records (e.g. using artificial intelligence and machine-learning algorithms) to drawing biologically relevant conclusions from the patterns within them (e.g. through comparisons to simulated null models), are arguably just as important advances as those in the monitoring technologies themselves (Krause et al. 2013; Kays et al. 2015).

Vast amounts of data are also produced by citizen science. Thanks to the development of the Internet, computational techniques and statistical tools, computers, and accessible interfaces now allow people passionate about wildlife to contribute to long-term field studies. Thus, beyond biologists, research projects are engaging millions of individuals worldwide in collecting data (see e.g. <https://www.ukbms.org> for the UK Butterfly Monitoring Scheme). The number of citizen science projects has exploded since 2000, and volunteers gathering data have already contributed to deliver significant insights into the ecological effects of climate change (e.g. Bonney et al. 2014; Isaac et al. 2014). Even more recent, modern computational science techniques are opening up the opportunity for ‘iEcology’ which aims to monitor populations through passively generated internet data, such as

using millions of Google search users' activity to infer bird species' occurrences or analysing Wikipedia users' locations to assess fish migration patterns (Jaric et al. 2020).

Thus, it is essential that biologists/ecologists continue to 'keep pace' with these data analytical techniques at the same rate that they adopt new data collection methods and new approaches to provide usable data storage on large scales, which have been developed for various long-term studies (Marshall et al. 2018). There is important incentive for ecologists to work more closely with engineers, computer scientists, and data scientists. Cross- and interdisciplinary work offers promising avenues for future developments in algorithms to process big data. Once the data have been gathered, processed, and stored, the question of access to these data is a final and important challenge to consider (Mills et al. 2015; Whitlock et al. 2016). Whether such databases should be open-access and available for usage by all or whether certain restrictions should be applied in an attempt to favour the continuation of these systems is currently under much debate. Although such consideration is obviously very useful, the rapidly growing trend towards unrestricted and immediate access to data across biology (Farnham et al. 2017; Culina et al. 2018; Sarabipour et al. 2019) suggests that open access to such data is not only valuable but inevitable, and emphasis should now be placed on establishing approaches to recognise and maximise the benefits of this for individual-based long-term studies.

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