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# What Have Long-Term Field Studies Taught Us About Population Dynamics?

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## Abstract

Long-term studies have been crucial to the advancement of population biology, especially our understanding of population dynamics. We argue that this progress arises from three key characteristics of long-term research. First, long-term data are necessary to observe the heterogeneity that drives most population processes. Second, long-term studies often inherently lead to novel insights. Finally, long-term field studies can serve as model systems for population biology, allowing for theory and methods to be tested under well-characterized conditions. We illustrate these ideas in three long-term field systems that have made outsized contributions to our understanding of population ecology, evolution, and conservation biology. We then highlight three emerging areas to which long-term field studies are well positioned to contribute in the future: ecological forecasting, genomics, and macrosystems ecology. Overcoming the obstacles associated with maintaining long-term studies requires continued emphasis on recognizing the benefits of such studies to ensure that long-term research continues to have a substantial impact on elucidating population biology.

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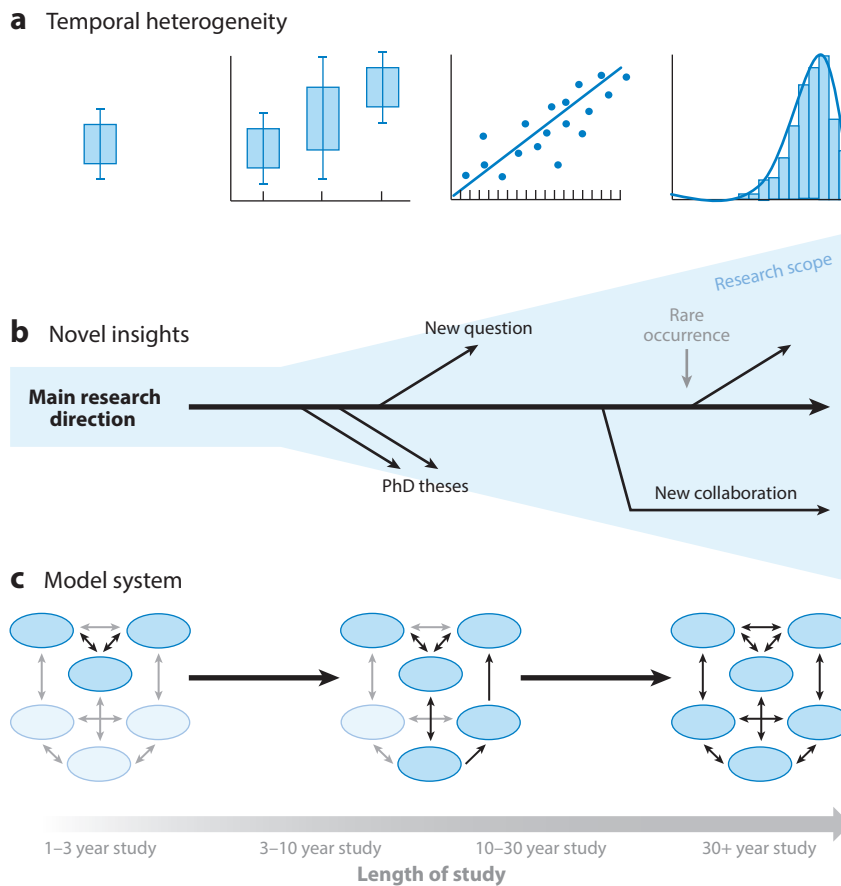
## 1. INTRODUCTION

Long-term studies have been, and will continue to be, instrumental in steering the study of population dynamics. When collecting specimens from exotic locales and cataloging identified species was the way natural science was practiced, Margaret Morse Nice began banding and studying the lives and behaviors of birds in her backyard (Morrison et al. 2018). Her multiyear work on individual song sparrows shifted the study of ornithology away from list chasing and toward a more integrative biology that incorporates life history, behavior, and population dynamics (Trautman 1977). Her thorough scouring of the literature combined with her diligent field observations of marked birds allowed her to describe the life histories of bird species in hundreds of articles (Langenheim 1996, Trautman 1977), directly address popular misconceptions (e.g., Nice 1953), and propose novel theories of territoriality and spatial dynamics (Nice 1941) that are still being cited today (e.g., Tingley et al. 2016, Tomasevic & Marzluff 2018). Niko Tinbergen wrote to Nice in a letter, "…you have become known to ornithologists throughout the entire world as the one who laid the foundation for the population studies now so zealously pursued" (Trautman 1977, p. 438; see also Langenheim 1996).

Nice's story did not remain anomalous. Long-term field studies of animal populations have been crucial throughout the development of ecology and evolution as disciplines (Clutton-Brock & Sheldon 2010, Magurran et al. 2010) and are increasingly recognized as essential for conservation biology as well (Conde et al. 2019). Designing and maintaining long-term field studies requires significant planning, dedication, funds, and time. Early career researchers may be increasingly unlikely to undertake this type of field research since laboratory experiments and short-term fieldwork can yield more immediate results that enable quick publication. However, long-term field studies can be equally appealing avenues of research that continue to be productive through time and are crucial for informing ecological, evolutionary, and behavioral aspects of population dynamics. The extended tenure of long-term studies allows for the observation of stochastic processes not easily replicated in laboratory settings, leading to new questions even after decades of work. Partially because of this, long-term field studies are also more likely to lead to novel insights not anticipated by the initial questions. The result is that as the depth and breadth of knowledge increase across multiple facets of a system, long-term study sites become model systems (i.e., richer intellectually and more popular with scholars) that allow us to answer fundamental scientific questions and test hypotheses. These three key aspects—observing heterogeneity, cultivating novel insights, and developing model systems—allow long-term studies to exert an outsized impact on our understanding of population dynamics (**Figure 1**).

We develop these ideas further in the following sections using three long-term study systems to illustrate how these ideas emerge in actual field studies. Given the sheer magnitude of research that has arisen from each study system, we cannot comprehensively present the decades of insights generated from all three. Instead, we discuss particular papers, ideas, and research directions arising from these study systems. We follow this presentation with a discussion of emerging research areas that can leverage these inherent aspects of long-term studies in the future. We focus on three broad conceptual areas that incorporate population dynamics—ecology, evolution, and conservation—with an example system for each area. Of course, these areas are not mutually exclusive because eco-evolutionary processes can influence species conservation (Knapp et al. 2016). However, they do illustrate broad scientific areas where population dynamics have a crucial role in theory and application. Ecology, evolution, and conservation all incorporate the concepts of demography, population growth rate, life history, and fitness, and they integrate other fields of biology (behavior, genetics, physiology, systematics, etc.) to understand how populations function. At the same time, the ways in which these concepts and fields are employed to make inferences

**a** Temporal heterogeneity

**b** Novel insights

Research scope

**Main research direction**

New question

PhD theses

Rare occurrence

New collaboration

**c** Model system

1–3 year study       3–10 year study       10–30 year study       30+ year study

**Length of study**

**Figure 1**

(*a*) Long-term studies incorporate more heterogeneity as time passes, allowing for an increased understanding of variance in the data. (*b*) The scope of long-term studies widens, yielding novel insights, as studies progress. All arrow end points represent novel insights. (*c*) Long-term studies can become model systems when relationships between elements are well characterized. These systems can then be used to test theories and predictions from other systems.

differ. Our focus is on field studies and long-term study systems. Although these concepts apply broadly to plants, invertebrates, and even microbes, our review is focused primarily on vertebrates, our area of taxonomic expertise.

## 1.1. Long-Term Studies Are Necessary to Understand Variation

Field studies are crucial to the study of population processes for most species and systems. They allow questions about how populations function to be answered in relevant environmental contexts. For some questions and for some species it is possible to adequately test a hypothesis in a short study over a single season or two. However, long-term studies are necessary when the research direction relates to or is influenced by temporal variation. Temporal variation—also referred to as temporal heterogeneity, environmental variation, or stochasticity—may itself be the target of investigation in some studies. In other cases, extended time allows observation of an ecological

or evolutionary relationship. With temporal heterogeneity in mind, we can define study length using the number of relevant temporal intervals over which a study occurs. In many cases, the annual cycle defines the most significant unit of time (e.g., annual breeding, seasonality, minimum generation time), and thus these intervals are years. Relevant time intervals may be shorter for other species (e.g., a small mammal or insect, which can have multiple generations occurring within a single year) or longer. For example, the number of generations or life spans may be more appropriate when measuring heritability of traits or patterns of actuarial senescence. In all cases, a key aspect of what makes a study long-term is the ability to observe and understand temporal variation.

As a starting point for highlighting the importance of using long-term studies to measure temporal variability, it is useful to work from first principles. The types of population processes that we can observe will vary with different time series lengths (**Figure 1a**). This can also be considered an exercise in statistical estimation in which inference depends on the number of degrees of freedom available to estimate a process. Studies that make only a single observation can begin to characterize important demographic measures, such as fecundity and size or age distribution, and, with a single revisit, can begin to estimate dynamic parameters including survival and population growth rate. This observation will consist of a single estimate with no measure of temporal variability and represents one specific time frame. This information alone may be sufficient to characterize the basic natural and life history of a species or to approximate the selection strength associated with changes in reproduction or survival. This approach could provide key insights into the structure and basic life history of a population or species and contribute to our understanding of its natural history. However, even if a variable, such as population growth rate, can be measured with a single data point, it will almost certainly be impacted by environmental variance and therefore require more time points to shape a true understanding of population processes (Lawson et al. 2015). Once observations are extended for another time interval or two (i.e., the typical length of many short-term studies), it is possible to determine whether these parameters vary. However, there are still no degrees of freedom available to estimate the relationship of this variation to an ecological or environmental variable or to measure the actual magnitude of the variation.

Not until a study reaches somewhere between 5 and 20 time intervals is it even possible to estimate the relationship of temporal variation with ecological and evolutionary processes. For example, time series of at least this length (and often longer) are needed to estimate temporal changes in dynamics, such as trends in population change or actuarial senescence (Colchero & Clark 2012, Gerrodette 1987, Warner et al. 2016). Studies of at least this length are also necessary to link temporal variability in population dynamics to a predictor variable such as climatic variation (Miller et al. 2011, Muths et al. 2017, Schwanz et al. 2010) or population density (Kaminski & Gluesing 1987, Lande et al. 2002). If generation time is short enough, such a study length may also permit better estimates of quantitative genetic parameters and predictors of variation in selection coefficients (Kruuk et al. 2000). When applied to conservation efforts, studies of this length enable observation of population responses to environmental stressors (assuming a shorter temporal distribution) as a function of management actions (Kendrick et al. 2015). In each case, temporal heterogeneity provides the sample units necessary to test predictions about the influence of variation on population-level processes.

In some cases, even longer time series are necessary to estimate population processes. These can include cyclic processes, interactions among multiple drivers, changes in system state, density dependence when population fluctuations are small, and hard-to-estimate ecological relationships, such as trends when noise is strongly autocorrelated (e.g., de Valpine & Hastings 2002, Stenseth et al. 1997). Other parameters can be accurately quantified only when the sample size is greater than a few dozen sample points. For example, the magnitudes of variance and

covariance in demographic rates have important implications for population dynamics and evolutionary processes (Boyce et al. 2006, Haridas & Tuljapurkar 2005). However, an accurate estimation of variance and covariance, let alone whether the variation is consistent with a given distribution (e.g., multivariate-normal variation), requires much larger sample sizes than are needed to estimate a mean or a simple linear relationship. Similarly, large time series are required to understand whether extreme events have outsized effects on population processes (Parmesan et al. 2000, Williams et al. 2015). Observing extreme events and estimating their frequency can only be done when observations occur over multiple time intervals. Doak et al. (2008, p. 953) define extreme changes in "the abundance of one or more species resulting from a previously unknown or unanticipated process" as an "ecological surprise." They argue that these types of surprises are quite common, but they must be well documented to adequately incorporate them into forecasting models or conservation decisions (Doak et al. 2008). Long-term studies can provide the necessary data sets for identifying and understanding these patterns.

## 1.2. Long-Term Field Studies Are Fertile Ground for Novel Insights

Population dynamic studies may be initially designed to address any of the specific variables mentioned above: fecundity, size and age distribution, survival, etc. However, as the time series of the study expands, more research questions may be asked within the system. This expansion of research scope will result in insights that could not have been anticipated at the beginning of the study (**Figure 1***b*). Long-term studies are likely to yield novel insights because extended work in a system will spark new research directions, new investigators will become involved in the system, and the opportunity to observe a rare event increases.

Long-term field studies provide a data-rich framework that will naturally provide more information through time. This information will include more temporal heterogeneity (as described above) but is also likely to include more breadth (i.e., more measured variables). Because scientific inquiry (and any individual research program) inherently builds on previous work, research questions and hypotheses will and should be modified through time. These modifications will often result in new questions being asked that deviate from the initial research direction. Concurrently, additional measurements or data of different scales are likely to be collected as the study progresses. Methodological advancements (e.g., small, affordable data loggers that continuously record temperatures have largely replaced manual daily measurements), improved theoretical models that warrant ground-truthing in the field, or unexpected results may cause researchers to reevaluate hypotheses and subsequently collect additional data. For example, the surprising conclusion that nesting behavior was significantly heritable in a turtle with temperature-dependent sex determination (TSD) only after warm winters was possible solely because multiple decades of behavioral, genetic, and environmental data were available (McGaugh et al. 2010). When initial estimates of heritability were unexpectedly low, McGaugh and associates (2010) were able to incorporate concurrently measured temperature data into their analysis to reveal that warmer winters induced additive genetic variation for both choice of nest location and timing of nesting activity.

Although conceivably true for all studies, field research is especially likely to involve multiple individuals at all career stages (undergraduate students, graduate students, postdoctoral researchers, collaborators, the public, etc.). Therefore, a long-term study will involve a shifting group of individuals who can provide new ideas, conduct side projects, and ask novel questions within a single study system. This cast of investigators will innately generate new research directions that yield novel insights and expand the scope of the study. For instance, investigators may hire postdoctoral or other early career researchers with skill sets somewhat divergent from their own to maximize this possibility.

Probabilistically, a long-term field study is also better positioned than a short-term study to capture a rare event that can illuminate a novel insight. A rare event may be intrinsic or extrinsic to the species being studied; a behavior that is seldom observable by researchers or practiced by the study species may constitute an intrinsically rare event, while an invasion, introduction, or catastrophe may constitute an extrinsically rare event. For example, when conducting a long-term study of spotted hyenas in Tanzania, Marion East and associates witnessed 13 adoptions of cubs by surrogate mothers among hundreds of family units (East et al. 2009; M.L. East, personal communication). Using these rare cases, they tested the impact of pre- and postnatal maternal effects on offspring social status (East et al. 2009). Without data spanning individual lifetimes that incorporated detailed observations of parental care and information on individual relatedness, this type of study would not have been possible. Examples of an extrinsic rare event may include the introduction of a disease, a population bottleneck caused by an extreme weather event, or a modified niche due to development or another anthropogenic disturbance. In these cases, having individual- and population-level data from before and after the event is invaluable in assessing ecological and evolutionary impacts on organisms and is likely to result in unanticipated insights (e.g., Jergenson et al. 2014). Additionally, these types of rare events can have lasting impacts on populations, so understanding their effects is integral to studying ecological and evolutionary processes within a system.

### 1.3. Long-Term Field Studies Are Necessary to Develop Model Field Systems

Long-term field studies focused on population biology are analogous to model species used to study developmental biology, genetics, or biomedicine. Model species are important because they provide considerable tractability (typically because of the ease of rearing individuals in the laboratory, a short generation time, and well-understood basic biology) for researchers to conduct deeply informed studies in different research groups and with broadly divergent approaches. These results yield either general insights across taxa or a starting point for comparative work. Most long-term field studies do not reach this point; a model field system in the context of long-term field studies emerges only when data on many diverse core aspects of basic biology are collected and studied over time. In these cases, long-term field studies engender complex but predictable systems in which to test important theories. They further produce generalizable information about population dynamics such that new methods and concepts can be robustly tested in systems in which dynamics are well characterized. Long-term studies can also effectively answer broad and complex questions in a well-understood contextual setting while still incorporating environmental variation and stochasticity, which is typically not possible in artificial settings. Finally, model field systems cultivate the development of novel methodologies, both field and analytical, that can then be applied in other systems.

As with a model species approach, the foremost characteristic of a model field system is that the basic biology is well characterized. Knowing a handful of characteristics and how they interact does not elevate a system to the level of a model, even if it might serve as such for addressing a narrow set of questions. Instead, a wealth of knowledge of the basic biology, coupled with the role of environmental heterogeneity and the emergence of novel insights from long-term field studies, can be leveraged to tackle fundamental problems that cannot be as powerfully addressed in other systems (**Figure 1***c*). Critically, the "devil is [often] in the detail" (Benton et al. 2006, p. 1173), and understanding the complexities of any system is necessary to make accurate predictions that are the foundation of demographic models, population viability analyses, and so on. At the same time, in the context of population dynamics, a model field system should embody population-level aspects (adult sex ratio, life span, etc.) that might be atypical yet allow for authoritative testing of

major hypotheses to yield principles generalizable across systems. A long-term field study assumes the status of a model field system only if it also encapsulates organismal life spans and adequately captures the impacts of environmental stochasticity to which wild systems are exposed, even if infrequently. In this way, long-term field studies can assume model field system status by revealing how population dynamics change across generations as well as within them, thereby providing a platform for robust tests of theory. We argue that such systems are no less important for advancing our understanding of population dynamics than are model species such as the mice, *Caenorhabditis elegans*, *Drosophila*, *Arabidopsis*, and zebrafish used for genetic and biomedical studies. In fact, both model species and model field studies can be accurately encompassed under the term model systems. We highlight three such model field systems in Section 2.

## 2. MODEL FIELD SYSTEMS

### 2.1. Ecology and Long-Term Field Studies

The Soay sheep of St. Kilda, Scotland, are likely direct descendants of Neolithic sheep and are the most primitive domestic sheep breed in Europe (Boyd et al. 1964) (**Figure 2a**). They have freely inhabited the isles of St. Kilda since its human population evacuated in 1930 (Boyd et al. 1964). In the past 60 years, these sheep have become key to increasing our understanding of age- and sex-specific population cycling (Coulson et al. 2001), the costs of reproduction (Clutton-Brock & Sheldon 2010), senescence (Hayward et al. 2013), and selection in the wild (Festa-Bianchet et al. 2017). The closed island system, individually tagged animals, multiple censuses per year,



**Figure 2**

(*a*) Soay sheep (*Ovis aries*) on St. Kilda, Scotland. Photo provided by Arpat Ozgul. (*b*) Medium ground finch (*Geospiza fortis*) on Daphne Major, Galapagos. Photo provided by B. Rosemary Grant. (*c*) Yellow-legged frog (*Rana sierrae*) in the Sierra Nevada range, USA. Photo provided by Roland Knapp.

reliable pedigree information, and considerable phenotypic variability of the sheep make this system ideal for the study of population dynamics. The long duration of the research has allowed for the adequate incorporation of temporal heterogeneity, the discovery of novel insights, and its contemporary use as a model system.

Peter Jewell and associates studied cohorts of feral Soay sheep from 1959 to 1967 and discovered that the population wildly cycled, increasing quickly and then crashing often (Boyd et al. 1964). These crashes appeared to be due to a reduction in food availability, and a density-dependent model adequately explained the presence of the population crashes but did not explain their frequency (Grenfell et al. 1992). The study was reestablished in 1985, and as the time scale of available data increased, comparing the dynamics of the isolated populations of Soay sheep on various isles of St. Kilda allowed researchers to detect patterns of environmental stochasticity that contributed to population synchronicities (Grenfell et al. 1998). Weather events such as severe spring gales increased the likelihood of a population crash and interacted with density-dependent effects to influence population cycles (Grenfell et al. 1998). The population cycles were even better explained when age and sex effects were introduced into the model, demonstrating that demographic heterogeneity is an essential component of the population dynamics of Soay sheep (Coulson et al. 2001). Further work incorporated heterogeneity in vegetative growth (Clutton-Brock & Pemberton 2004, Clutton-Brock et al. 1991, Conradt 1999), weather events (Hallett et al. 2004), and climate (Berryman & Lima 2006, Milner et al. 1999).

Investigations into the proximate causes of population crashes in Soay sheep yielded surprising results. Although population crashes did ultimately occur because of interactions between demography and food availability, individual sheep mortality was caused by both starvation and extreme gastrointestinal parasite loads that led to nutritional deficiencies (Gulland 1992). Recognizing that parasitism may play a role in population dynamics, researchers have further investigated variables affecting nematode diversity, parasite loads, and parasite resistance (Craig et al. 2008, 2009; Hayward et al. 2010; Sinclair et al. 2016). By relating survival rates, parasitism loads, and microsatellite heterozygosity in Soay sheep, researchers revealed parasitism as a potential mechanism by which selection may act against inbreeding, thereby promoting genetic diversity, since more homozygous sheep were more susceptible to parasitism (Coltman et al. 1999). Further novel insights into social behavior, fitness tradeoffs with reproduction, genes that regulate biological clocks, the genetics of polymorphisms, and senescence were possible because of the long-term nature of the Soay sheep data set.

The variety of methods and approaches used to address research questions stemming from population cycling has resulted in the Soay sheep system being used as a model for multiple fields. For example, Stenseth et al. (2004) leveraged the Soay sheep system to create a method that identifies the interacting influence of climate and demography on population dynamics; this method was recently applied to coastal phytoplankton populations (Barraquand et al. 2018). Morrissey et al. (2007) developed an analytical framework to estimate pedigree error and sensitivity and used the Soay sheep system as a case study to demonstrate the efficacy of their approach. Although the paternal pedigree is questionable, the maternal pedigree of Soay sheep is highly accurate (Pemberton et al. 1999), which allowed Morrissey et al. (2007) to manipulate aspects of phenotype, heritability, and known parentage to test their framework. Finally, because of the relevance of Soay sheep to their domestic counterparts in industrial farming, the sheep have been used as a model system for studying traits that have potential commercial benefits. The extensive work on phenotypes and associated parasitism rates has allowed the Soay sheep system to be explored with candidate gene approaches (Brown et al. 2013) to identify genes related to parasite resistance (Wilkie et al. 2017). Soay sheep have also been studied to determine whether parasitism impacts diet selection for application to farmed breeds (Jones et al. 2006).

## 2.2. Evolution and Long-Term Field Studies

In 1977, Peter and Rosemary Grant began a field study on Daphne Major, Galapagos, to evaluate adaptive radiation in the 13 species of finch endemic to the islands, collectively referred to as Darwin's finches. Darwin collected the same species of finches on his *Beagle* voyage, and David Lack published seminal comparative work using that collection. However, the Grants' ensuing fieldwork has arguably contributed more invaluable information about evolution and natural selection in the wild, largely due to the long-term nature of their study. A combination of the preservation and popularization of the finches in Darwin's collection, the island system, and the Grants' intensive annual fieldwork documenting the morphology and natural history of the species has resulted in Darwin's finches being used as a model for speciation and observable evolution in the wild.

Over the first 20 years of the Grants' study on Daphne Major, periodic droughts and excessive rainfall affected the availability of seeds such that the direction of selection on beak size depended on environmental fluctuations (Gibbs & Grant 1987). These extreme environmental events, which would have been missed in short-term studies, reshaped what we thought we understood about natural selection and evolution; not only were changes in the direction of selection observable, but evolutionary processes were occurring at a faster rate than previously thought possible in the wild. Later, when severe El Niño events caused a population bottleneck on the island, the Grants observed hybrid vigor (Grant & Grant 1993) and subsequently demonstrated the effects of hybridization on the direction of evolution (Grant & Grant 1994). Extreme weather events are not the only type of heterogeneity to contribute to the evolution of Darwin's finches. Shortly after the study began, Peter Grant published a model of allopatric speciation to explain the diversity of finches (Grant 1981). The Grants later significantly amended their proposed speciation model to account for a changing environment (increases in vegetative complexity, available habitat and landmasses, etc.) based on another decade of data (Grant & Grant 2002), demonstrating the necessity for long-term data to adequately incorporate heterogeneity.

In late 1982, a breeding population of a species of finch (*Geospiza magnarostris*) appeared on Daphne Major from a neighboring island (Grant & Grant 2006). This species competed with *Geospiza fortis* (**Figure 2b**) for large seeds, and as the number of *G. magnarostris* grew, so did linear selection against large beak size in *G. fortis* (Grant & Grant 2006). This event represented the first known case of character displacement seen in action, rather than as an inferred outcome, and was possible because of the Grants' annual research trips to the island. Another rare event sparked more novel insights; the arrival on Daphne Major of a single individual of *G. fortis* with exceptional morphology (a large size and unusual song) allowed the observation of reproductive isolation and potential speciation in action (Grant & Grant 2009). Since these revelations, the Grants' finch system has also yielded insights into cultural inheritance (Grant & Grant 1996) and human impacts on diversification (Hendry et al. 2006).

The extensive study of Darwin's finches in the field, initiated and primarily pursued by the Grants, has led to the finches of Daphne Major being considered a model system that can be used to test hypotheses from other fields. Though known primarily for its contributions to models of speciation, directional selection, and hybridization, the finch system is also thoroughly developed enough to act as a model for other processes. For instance, Mallarino et al. (2011) used the finch system to investigate how two tightly correlated traits can become uncoupled developmentally. Using what is known about Darwin's finches, they identified candidate genes that are differentially expressed by various finch species during development, manipulated them in chickens, and used this information to infer tissue modules that likely regulate development and may be important elements in avian evolution (Mallarino et al. 2011). Morphological data on Darwin's finches were also used to construct early phylogenies (Schluter 1984), which were later assessed relative to

phylogenies constructed from molecular markers (Petren et al. 1999). Maintaining a well-understood, continuously monitored system was helpful (though arguably not essential) for informing and comparing the then-novel method of phylogenetic reconstruction using microsatellites to trees based on more traditional (i.e., morphological) data types.

## 2.3. Conservation and Long-Term Field Studies

Mountain yellow-legged frogs (actually comprised of two species: *Rana muscosa* and *Rana sierrae*) (**Figure 2c**) were once abundant in California (Adams et al. 2017). However, introductions of nonnative trout to lakes in the Sierra Nevada range contributed to dramatic declines in frog abundances (Knapp 2005, Knapp & Matthews 2016). Researchers, in conjunction with state and federal agencies, began studying the impact of game fish introductions and the ability of amphibian populations to recover after fish removal (Knapp et al. 2007, 2016; Vredenburg 2004). Populations of mountain yellow-legged frogs throughout the Sierra Nevada range have been monitored using visual surveys for more than 20 years to document their presence, abundance, and extirpation from specific lakes and regions. The frogs are now considered endangered, but research on management strategies, breeding programs, epidemiology, and conservation genetics provide potential for reestablishing the species. Recently, landscape-wide surveys have detected increased abundance across populations in Yosemite National Park (Knapp et al. 2016).

Because many mountain yellow-legged frogs occupy protected areas (Knapp & Matthews 2016), the impact of environmental stochasticity on populations can be disentangled from habitat disturbance or anthropogenic effects. For example, water depth significantly predicts the presence of mountain yellow-legged frogs (Knapp 2005), and subsequently, altered precipitation that results in drying or reduction of some bodies of water substantially affects the abundance and recruitment of mountain yellow-legged frogs (Lacan et al. 2008). Additionally, although many populations are in national parks, tissues from frogs in some of them have shown signs of pesticide accumulation from neighboring agricultural areas, demonstrating the need to consider landscape effects when designating protected areas for at-risk species (Fellers et al. 2004). Studying the abundance of mountain yellow-legged frogs also allowed researchers to detect changes in the abundances of species, such as the Sierra garter snake (*Thamnophis elegans*) and aquatic macroinvertebrates (Matthews et al. 2002, Smith et al. 2016), that are affected by various life stages of the frogs. By monitoring multiple populations throughout the range of the mountain yellow-legged frog, heterogeneity introduced by habitat variability, environmental differences, species richness, and time have been incorporated to obtain a comprehensive understanding of the needs of this endangered species.

While documenting the decline of mountain yellow-legged frogs in the Sierra Nevada range, researchers detected the emergence and eventual spread of chytridiomycosis, a disease caused by *Batrachochytrium dendrobatidis* (Bd) that is currently devastating amphibian populations worldwide (Vredenburg et al. 2010). In mountain yellow-legged frogs, there are two possible disease outcomes in populations: extinction and persistence (Briggs et al. 2010). Though most populations recently infected with Bd are quickly extirpated, some populations persist even with infection. Based on these observations, disease models were developed that potentially explain the persistence of frog populations as being due to density-dependent host–pathogen effects (Briggs et al. 2010, Vredenburg et al. 2010). Immunological studies have since identified antimicrobial peptides unique to the mountain yellow-legged frog (Rollins-Smith et al. 2006). Although these peptides do not appear to have a role in Bd resistance, temporins (one of the peptides identified in *R. muscosa*) may be valuable for the development of anti-infective and antisepsis drugs (Mangoni et al. 2007). Mountain yellow-legged frogs were also the first anuran found to host anti-Bd bacteria on their

skin that may contribute to controlling Bd outbreaks in persisting populations (Woodhams et al. 2007); the discovery of these bacteria in a frog has since sparked investigations into this mechanism of innate immunity in other anuran species (e.g., Bresciano et al. 2015, Holden et al. 2015, Madison et al. 2017). The rare occurrence of this devastating disease in the midst of a long-term study facilitated novel insights into disease models, immunology, and impacts of Bd.

The mountain yellow-legged frog system is unique in that, aside from the introduction of nonnative fish, their habitats are largely protected and remain directly unaltered by development. This allows them to be a model system for studying amphibian decline due to reasons unrelated to habitat loss and also permits semicontrolled field tests of Bd treatment. Additionally, the long-term fieldwork continuously carried out across their range has allowed the dynamics of their decline (and partial resurgence) to be mapped as it occurs, creating a robust data set for tracing disease and recovery dynamics (Joseph & Knapp 2018, Wilber et al. 2017). For instance, the disease dynamics recorded by researchers in mountain yellow-legged frogs in the Sierra Nevada range has been used to test a model for predicting the arrival and spread of Bd to other amphibian populations (Zhou et al. 2015).

## 2.4. Summary of Long-Term Field Studies

In Section 2 we present three examples of long-term field systems (Soay sheep, Darwin's finches, and mountain yellow-legged frogs) to illustrate what we argue are the three primary drivers that explain the substantial impact that long-term studies have on the study of population dynamics. All three systems benefited from heterogeneity that resulted in more accurate models, yielded novel insights from a combination of an increasing breadth of data through time (e.g., parasitism in the sheep population) and chance observations of rare events (e.g., the introduction of a single individual with extraordinary traits, the arrival of Bd), and have now become model systems for studying ecology, evolution, and conservation. We hope our ideas can be applied to ongoing field studies to further spread the benefits and emphasize the rewards of long-term fieldwork to population biology.

## 3. WHAT DO WE STILL HAVE TO LEARN FROM LONG-TERM FIELD STUDIES?

Long-term field studies arguably become increasingly important as the time over which they are being conducted increases, because each additional year can lead to a nonlinear gain in information and increases the likelihood of high-impact discoveries and publications (Clutton-Brock & Sheldon 2010). Furthermore, the emphasis of long-term field studies has shifted in recent years as, in particular, advances in evolutionary genomics and quantitative genetics have influenced the types of questions that can be addressed. In this section we highlight three areas that long-term field studies are likely to enhance in the next decade.

## 3.1. Predictive Ecology

A key goal of ecological research is the ability to predict how such systems will change through time (Houlahan et al. 2017). Accurate forecasting is especially crucial to address increasing impacts on ecological systems (Urban et al. 2016). As we have discussed, long-term field systems have long acted as important research laboratories for the conservation of species and ecosystems by informing management strategies and providing information for forecasting models. However, most ecological forecasts are never tested, and thus we know little about which methods lead to

accurate predictions. Long-term study systems therefore have the potential to be laboratories for testing forecasts and improving our ability to generate accurate predictions, especially in light of the occurrence of rare events. The ability to develop models based on long-term research (and associated heterogeneity), make short-term forecasts, test them, and continue to refine our models is crucial if we are to improve ecology as a predictive science (Dietze et al. 2018). The management of harvest in North American mallard populations is an excellent example of how predictive ecology can be accomplished with long-term research (Nichols et al. 2007). A need to sustainably manage waterfowl populations pushed researchers to develop predictive models based on long-term research to determine the strength of density dependence and the effect of take on population dynamics. These predictions are tested annually as new data are collected and the strength of evidence for alternatives is reevaluated and incorporated into future recommendations.

### 3.2. Genomics and Genetics

Most long-term field studies center on measuring the phenotypes of individual organisms in populations. However, with the expansion of molecular field-portable tool kits and accompanying analytical support, long-term field studies will be increasingly able to incorporate molecular, genetic/genomic, and community-wide information. In all three systems described above, contemporary genomic research projects have been integrated into the primary studies to address questions about traits and relationships between individuals and species. Importantly, this cutting-edge work can not only involve resident organisms in these systems but also leverage time series of collected tissues or environmental samples. Whether analyzing tissue samples to reconstruct pedigrees in wild populations to quantify microevolution (e.g., Bonnet & Postma 2018, Pujol et al. 2018), extracting eDNA from water samples to examine the time course of population changes or the arrival of invasive species (e.g., Adams et al. 2019, Piaggio et al. 2014), or tackling other key matters such as evaluating ecological correlates of the genetic structure of populations (e.g., Manier & Arnold 2006), ongoing long-term field studies are making important contributions to our understanding of population dynamics in heterogeneous circumstances. In this way, long-term field studies can readily transition into model systems that are superbly positioned to address long-standing conceptual questions with modern technology as well as unanticipated issues that arise as theory and empiricism advance. In the latter instance, for example, integrative long-term field studies would seem to be a requisite for the proper investigation of eco-evolutionary dynamics, an emerging field of inquiry (De Meester et al. 2019, Hendry 2019).

### 3.3. Macroecology

Development of ecological principles and predictions that can be generalized across systems requires the ability to examine processes across multiple dimensions (taxonomy, space, and time; McGill 2019). Long-term studies have served as the backbone for one of these dimensions, time, by measuring processes occurring on scales ranging from years to decades. When long-term systems are combined, they then include additional dimensions of spatial and taxonomic replication. Using networks of long-term study systems to answer macroecological questions has the potential to unlock new understanding of how ecological systems function and to clarify concepts that can then be generalized. These types of networks may include both those that were originally designed to be collaborative and those that combine independent studies with similar data types to ask broader questions. Examples of collaboratively designed networks that have been or will be important for identifying generalizable results include historic monitoring programs such as the North American Breeding Bird Survey and the Monitoring Avian Productivity and Survivorship

(MAPS) program (Saracco et al. 2012, Sauer et al. 2017), as well as initiatives such as the National Ecological Observatory Network (NEON) (Schimel et al. 2007) and the Salamander Population and Adaptation Research Collaboration Network (SPARCNet) that replicate study designs across large geographic ranges. Alternatively, other powerful networks of long-term studies have been formed from the merging of individual studies to ask specific questions about changes in biodiversity (Dornelas et al. 2014), the effects of climate change (Janzen et al. 2018, Miller et al. 2018), and demographic patterns in wild populations (Jones et al. 2014). Developing and facilitating networks of long-term research will ensure that long-term studies continue to thrive and will help address pressing basic and applied ecological questions.

## 4. CONCLUSIONS: THE FUTURE OF LONG-TERM FIELD STUDIES

Long-term field studies are typically appealing to the public and disproportionately inform policy decisions (Hughes et al. 2017). Nonetheless, this type of research is especially prone to lapses in funding (Clutton-Brock & Sheldon 2010). To best maximize the utility of long-term field studies and to develop them into model systems, it is important to make the raw data and metadata available. Although journal editors and funders essentially want data made available upon publication of analyses (e.g., Whitlock et al. 2010), some leaders of long-term field studies resist this data availability time frame and raise additional concerns about such policies (Mills et al. 2015). Resolving these conflicts is critical if long-term studies are to continue to steer the direction of ecological and evolutionary research. Creative solutions such as collaboration between users and data generators, longer data embargo periods, and archiving of only the data necessary for published analyses could alleviate most of the issues and maximally promote the utility of long-term field studies (Roche et al. 2014, Whitlock et al. 2016).

We argue here that three key ways that long-term studies are crucial to the study of population dynamics are that they are able to incorporate heterogeneity in a way short-term and laboratory studies cannot, they are likely to generate novel insights, and they have the potential to develop into model systems that can be used to test other ideas and move the field forward. Although long-term studies may currently be less likely to be undertaken by early career researchers and supported by funders, their importance, as demonstrated by the far-reaching impacts of the Soay sheep, Darwin's finch, and mountain yellow-legged frog systems alone, should not be underestimated. Indeed, fieldwork such as mark-recapture studies with no tissue sampling can be undertaken with modest funding while still yielding valuable data; such studies are viable options for involving citizen scientists to facilitate long-term continuation. Especially in the coming decades, long-term studies and study networks will uniquely advance predictive ecology, genetic and genomic features underpinning eco-evolutionary feedbacks, and the taxonomic breadth of fieldwork in macroecology, inevitably moving the field of population biology forward.

## DISCLOSURE STATEMENT

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