

The expanding value of long-term studies of individuals in the wild

Ben C. Sheldon, Loeske E. B. Kruuk & Susan C. Alberts



Over the past seventy-five years, long-term population studies of individual organisms in their natural environments have been influential in illuminating how ecological and evolutionary processes operate, and the extent of variation and temporal change in these processes. As these studies have matured, the incorporation of new technologies has generated an ever-broadening perspective, from molecular and genomic to landscape-level analyses facilitated by remote-sensing.

In early 1947, John Gibb and David Lack from the University of Oxford erected 100 wooden bird nest boxes in Marley Wood, the southeast corner of Wytham Woods, just west of Oxford, UK. Inspired by the work of Dutch ornithologists (specifically Wolda and Kluyver¹), who had shown that the great tit *Parus major* was a good model for avian population biology, Lack aimed to start his own population study. The

study of great tits (Fig. 1a) in Wytham Woods has continued uninterrupted for 75 years, generating records of the full life histories of almost 120,000 individual birds. The current descendants of those 100 original nest box inhabitants now have their social relationships monitored by radio-frequency identification (RFID) tags, their genomes sequenced, and the timing of budburst in their chosen nesting trees monitored by drones. Many other individual-based studies of bird and mammal populations were founded in the following decades. The past year has seen important landmarks for some of these studies: the Amboseli Baboon project (Fig. 1b; founded by Jeanne and Stuart Altmann) celebrated its 50th year in 2021, and the Rum Red Deer study (Fig. 1c; founded by Tim Clutton-Brock and Fiona Guinness) reached 50 years in 2022 (ref. ²), as did the Isle of May European shag study, founded by Mike Harris and Sarah Wanless. These are examples of several dozen continuing studies that are globally distributed. Collectively, many thousands of scientific papers have resulted from these studies³ and they continue to generate scientific insight into an ever-broadening range of contemporary questions in ecology and evolution, and their wider intersections with global challenges.

The questions asked in the field have changed fundamentally over the intervening years, partly because of the information that these studies has generated – and the methods available for study have arguably changed even more so. At least some of the studies were founded before the role of DNA as hereditary material had even been fully identified,

Fig. 1 | Classic models in the development of long-term population studies of individuals in the wild. a, Great tit (*Parus major*) in Wytham Woods near Oxford, UK; study founded in 1947. Photograph credit, S. Evans. **b**, Group of baboons (*Papio cynocephalus*) at Amboseli, Kenya; study founded in 1971. Photograph credit, N. Snyder-Mackler. **c**, Red deer (*Cervus elaphus*) on Rum, Inner Hebrides, UK; study founded in 1972. Photograph credit, A. Morris.



when statistical analysis was much less complex, biologging did not exist as a concept, and current digital techniques in data collection and analysis were undreamt of. In this Comment, we explain the success of long-term population studies of individuals, challenges to their viability, and key emerging questions and approaches.

Insights into processes and change

Long-term individual-based studies have been conducted across a range of biomes and life histories, from remote sub-Antarctic islands⁴ to tropical savannah⁵, and from heavily human-modified landscapes to more-or-less undisturbed boreal forest. However, despite this diversity, an undeniable bias towards Northern Hemisphere (and in particular, North American or European) study populations persists. Taxonomically, studies have also traditionally been biased towards avian and mammalian systems, although more diversity is increasingly apparent, including insect, fish, reptile and plant models^{6–9}. The core elements of these studies are (1) identification of known individuals in a well-defined study population; (2) monitoring of such individuals across entire lifespans, from birth to death, and across multiple generations; (3) standardized collection of core data across years; (4) elucidation of genetic relationships within and between generations, either by observation or, more often now, using parentage analysis with genetic markers; and (5) collection of fine-scale biotic and abiotic environmental data. On top of this framework are then mapped multiple additional types of data, ranging from physiological, parasitological and immunological data to fine-scale behaviour and social organization data. These core elements then allow the estimation of individual fitness and its sources of variance.

This basic framework seems simple enough, but it allows us to address many questions about ecological and evolutionary processes in natural populations. What characterizes the scientific approach that has been enabled by the patient collection of these long-term data? We argue that they enable, above all, two particular types of inquiry that are important for our understanding of organisms in nature. First, because of their continuous nature and the ability to track outcomes far downstream, they enable the study of processes rather than simply states or events. For example, longitudinal datasets from long-term populations have enabled an increasingly rich characterization of the way that ageing develops across traits, between the sexes and within different groups of populations¹⁰. They have also enabled analysis of the links between age and fitness across generations and the physiological and behavioural links between ageing and early-life experiences. Such studies also allow us to understand the systems by which sets of processes are connected to each other through interactions, correlated responses, cascades and constraints. For example, in Soay sheep on St Kilda, lambs born after warm and wet winters are lighter and have lower juvenile survival and later age at maturity, but higher survival once they reach adulthood¹¹. The integrated view of processes that results from such studies enhances our understanding of ecology and evolution.

Second, long-term individual-based studies allow analysis of variation and change in the processes. In particular, their longevity enables the analysis of the effects of changing environmental conditions (in particular, those due to current changes in the world's climate), and the partitioning of responses to these changes into evolutionary, ecological and behavioural components. For example, a long-term individual-based study of the alpine plant moss campion, across a wide latitudinal gradient, has revealed that survival in all age classes declines with warmer temperatures near the species' southern range

limits, but individuals in the youngest age classes grow more rapidly at these warm southern limits⁹. The combination of these two processes results, over time, in demographic buffering that may help to slow – though may not ultimately prevent – extinction as the climate warms. As another example, the advance in breeding time observed in red deer on Rum has been shown to be due in roughly equal parts to a plastic response to warming temperatures and an adaptive evolutionary response to natural selection favouring early breeders¹².

Because data in these studies are collected following standardized protocols from year to year, they can generate large sample sizes for analysis of variation in individual fitness in different environmental conditions. The longest-running studies now enable analyses of population- and individual-level responses, and the estimation of the sensitivity of selection, to annual variation over more than five decades. For example, the Wytham great tit study provided some of the earliest evidence of clear phenological responses to changing climate (with nesting dates advancing as spring temperatures warmed¹³), and has enabled the teasing apart of the roles of phenotypic plasticity and environmental drivers in underpinning this response spanning the period from the 1960s to today^{14–17}.

Many long-term studies include archives of blood, tissue or faecal samples, often collected for parentage or endocrine analyses. As laboratory techniques have developed and become possible at scale, these samples have become valuable for other purposes. For example, the need to assign paternity in the long-term studies of red deer and Soay sheep studied for 87 years collectively has resulted in multigenerational banks of blood samples that have supported increasingly high-resolution genomic analysis of the causes of phenotypic trait variation and inbreeding depression, variation in recombination rate, and genomic causes of selection^{18–20}. Collection and storage of individually recognizable red deer antlers has provided DNA samples for males for whom blood samples were not available, sometimes decades after antlers were originally shed¹⁸. Similarly, long-term curation of faecal samples in the Amboseli baboon study began in 2000 for both parentage and endocrine analysis, resulting in tens of thousands of banked samples. Recently, these samples have been used to shed unprecedented light on longitudinal stability and change in individual gut microbiomes over time, and to identify both genetic and ecological drivers of gut microbiome dynamics^{21,22}.

What of the future?

Long-term studies have taught us that future uses may not always be easily predicted, but that gaining new biological insight is greatly enhanced by having systems in place that enable access to long-term data. For example, the founders of long-term studies in the 1940s to 1960s may not have considered the potential for their data to be used to understand the effects of changing climates, even if some of the earliest research focused on external environmental drivers of population-level variation. Just as genomic technological advances have led to numerous new insights in the past decade^{7,23,24}, applications of new technologies will further increase the value of long-term studies in the coming decades. One example is the widespread application of machine and deep learning, for applications as diverse as photogrammetric identification, automated acoustic monitoring, inference of behavioural states from biologging data and video analysis of social behaviour. Another example is the combination of richly detailed individual and environmental data with new forms of earth observation, from autonomous low-level drones to global satellites, which – particularly when combined with biologgers of increased

sophistication – will enable analysis of behavioural responses to the environment in unparalleled detail.

One new theme that is already emerging in long-term studies is the pooling of data across studies to obtain more general insights and increased scale. De Villemereuil et al.²⁵ used data from 39 populations of 21 species of birds and mammals to show that natural selection on breeding phenology is modulated by plasticity enabling populations to track a moving optimum. Bailey et al.²⁶ analysed 67 populations of blue and great tits across Europe to show a large-scale negative correlation between the responsiveness of populations to climatic variation and their past exposure. Lastly, combining data on individual fitness from nearly a quarter of a million individuals across 19 populations of 15 species of birds and mammals with new statistical methods, Bonnet et al.²⁷ showed that additive genetic variance for fitness in natural populations is more extensive than previous studies suggested. The result implies the capacity for rapid evolutionary adaptation in contemporary populations, but also that adverse effects of current environmental conditions must be countering current ongoing adaptation. The ability to scale from observations at the level of individuals to those across populations distributed across the majority of the geographical range of some species promises new insights about the spatial scale and temporal coherence of phenotypic variation and natural selection, as well as differential effects of climate change over large-scale regions. Formal frameworks (for example, SPI-Birds²⁸) have been designed to enable collaborations involving such data. However, these lack long-term funding support, and mechanisms to secure their future would be valuable.

Challenges

The future of the individual long-term studies, even those that are longest-established, is not always secure. In general, funders have typically not prioritized the maintenance of such work in its own right as a priority, and most such studies have been funded by long runs of back-to-back short-term grants. Because continuous monitoring is essential, the process forces researchers to walk a tightrope of unbroken grant-raising success in an increasingly competitive funding environment. The nature of such funding opportunities often emphasizes short-term goals rather than the long-term benefits of observational research, creating a tension between studying an unperturbed system versus undertaking short-term experimental manipulations. Reviewers can (and sometimes do) question whether new questions could be asked with the data already collected, rather than by funding further field data collection. We argue that such responses are short-sighted, especially in the context of the ongoing and unknown future effects of climate change for which long-term continuity is essential. Low-level funding that ensures continuity of data collection is available to some researchers (in particular, the NSF's Long-Term Research in Environmental Biology (LTREB) system). However, in general, unlike the physical sciences (where funding mechanisms operate over decadal scales), it seems that ecological and evolutionary science has not yet appreciated

the value of really long-term funding frameworks. Finally, for the field, an important collective challenge also remains to address the taxonomic and geographical diversity of long-term studies.

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Competing interests

The authors declare no competing interests.