Review

Special Issue: Long-term ecological research

Feature Review

Individuals and populations: the role of long-term, individual-based studies of animals in ecology and evolutionary biology

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Many important questions in ecology and evolutionary biology can only be answered with data that extend over several decades and answering a substantial proportion of questions requires records of the life histories of recognisable individuals. We identify six advantages that long-term, individual based studies afford in ecology and evolution: (i) analysis of age structure; (ii) linkage between life history stages; (iii) quantification of social structure; (iv) derivation of lifetime fitness measures; (v) replication of estimates of selection; (vi) linkage between generations, and we review their impact on studies in six key areas of evolution and ecology. Our review emphasises the unusual opportunities and productivity of long-term, individual-based studies and documents the important role that they play in research on ecology and evolutionary biology as well as the difficulties they face.

Long-term studies at different biological levels

A central problem in studies of animal ecology and evolution is that many of the most important ecological and evolutionary processes affecting populations, including the demographic processes controlling animal numbers and the evolutionary processes generating adaptation, commonly occur over multiple years or decades rather than across hours, weeks or months. Studies of naturally regulated populations that provide data that extend over adequate periods of time are consequently crucial to research in many areas of ecology and evolutionary biology. Here, we describe the two main categories of long-term studies of animals, briefly review their achievements in six key areas over the past thirty years, assess their productivity and outline the challenges they face.

Population-level studies

Longitudinal studies of animal populations fall into two main groups. First there are studies at the population level that measure the size, structure and distribution of particular populations but do not monitor individually marked or recognisable animals. Records of density and distribution extending over three or more decades are available for populations of an increasing number of invertebrates [1] and non-human vertebrates [2,3], especially birds [4]. These studies provided the basis for the first investigations of the regulation of animal numbers [5] and have continued to play an important role in research on the demography and dynamics of animal populations [2,6–9]. In several cases, detailed records of the timing or geographical distribution of changes in population size have provided important insights into the effects of human activities on animal populations: studies of the effects of DDT on the fertility of raptors [10,11], of discarded oil on sea birds [12], of discarded lead shot on waterfowl [13] and of the consequences of long line fishing on sea birds [14] are obvious examples. More recently, long-term studies of animal populations have provided crucial evidence of the effects of changes in climate on distribution, density, growth and reproductive timing in different organisms [9,15–18]. For example, a recent analysis of changes in reproductive timing from 726 terrestrial, freshwater and marine taxa in the UK reveals an accelerating tendency for reproductive seasons to begin earlier. This effect is less pronounced for secondary than primary consumers, heightening the potential risk of temporal mismatches in key trophic interactions [19] (Figure 1).

Although longitudinal studies at the population level have an important role to play in ecological studies, they have serious limitations. They often have difficulty in identifying the proximate causes of change in population size, since it is usually difficult to distinguish between the effects of changes in breeding success, survival, emigration and immigration. Many environmental factors affect animals at particular stages of their life history and because of this, accurate predictions of change in population density require knowledge of the age structure of populations and the effects of age on breeding success and survival [20]. However, accurate ageing is frequently difficult, particularly for older categories and attempts to assess the effects of age on demographic parameters are frequently further

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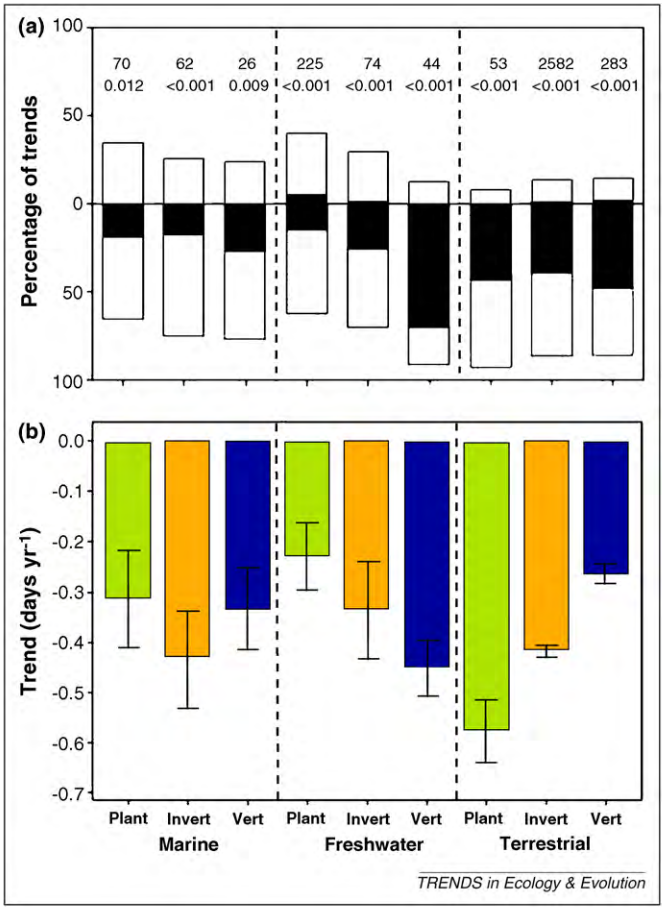

Figure 1. Changes in phenology in UK plants, invertebrates and vertebrates in marine, freshwater and terrestrial environments between 1976 and 2005 [19]. **(a)** percentage of phenological trends in each taxon by environment combination. Trends below the horizontal line are advancing and those above it are delaying. Black bars indicate statistically significant trends. Total sample sizes and probability values are given above each bar. **(b)** mean plus or minus SEM of rates of change for plants, invertebrates and vertebrates. Reproduced from *Global Change Biology.*

complicated by biases due to the selective appearance or disappearance of different categories of animals at different stages of the life history [21,22].

The limitations of population-level data are even more important in evolutionary studies. While repeated sampling of the genetic structure of populations can provide estimates of changes in the relative numbers of different phenotypes or genotypes [23,24], the insights that it offers into the biological causes of change are often limited, unless these have been established either by experimental or observational studies at the individual level. In particular, longitudinal records of individual life histories are usually necessary to assess the fitness costs and benefits of different traits or breeding strategies, since particular actions or events can have deferred consequences for breeding success or survival at other stages of the lifespan [25,26]. In addition, population level studies are severely limited in their ability to explore the effects of social behaviour on reproduction and survival and their ability to explain the evolution of reproductive strategies is very limited.

Individual-based studies

The second category consists of long-term studies that are able to monitor the development and life histories of samples of individually recognisable animals (Box 1). Records of this kind make it possible to avoid many of the limitations of population-level data described above and have six characteristics of central importance in studies of ecology and evolution. First, they provide a reliable basis for documenting age-related changes in life history parameters. Since the age of individuals affects virtually all aspects of their behaviour, reproductive performance and survival, the ability to identify and assess age effects is of fundamental importance in exploring and interpreting the effects of environmental parameters on breeding success and survival. It is also of importance when investigating how these effects interact with individual differences in phenotype or genotype, especially in longer-lived animals. As a result, studies that explore ecological and evolutionary process but fail to take the effects of age into account are often likely to reach misleading conclusions.

Second, longitudinal studies of individuals make it possible to connect events at one stage of the life history to those at another, providing insights into the causes of variation in growth, breeding success and survival. For example, studies of vertebrates (including humans) have demonstrated the substantial effects of differences in early development on breeding success, survival and longevity in adults [27,28] and have shown that such differences can generate contrasts in breeding success or survival between cohorts and induce changes in population size several years after the events that caused them [29,30].

Third, individual-based studies provide opportunities to document the kinship structure of populations and to assess the effects of social relationships on survival and breeding success. In many animal populations the social status of individuals and their relationships with other group members have an important influence on their survival and breeding success as well as on the breeding success of their offspring, with important implications both for population demography and for the evolution of social behaviour [31–33]. In some animal societies, these relationships are strongly influenced by the effects of kinship on the tendency of individuals to cooperate or compete [34,35]. In other cases, the history of relationships between individuals exerts an important influence on their behaviour. For example, in some birds, partners commonly abandon mates with whom they have failed to breed successfully or which have mated outside the pair [36,37].

Fourth, long-term, individual-based studies make it feasible to measure the extent to which breeding success differs between individuals and their offspring and to assess the causes of these differences. Consistent individual differences in breeding success are common, especially in relatively long-lived multiparous species, generating large differences in lifetime reproductive success between individuals that drive selection on particular traits and can have important consequences for population dynamics and demography [25,38,39]. Successful individuals are often less affected by adverse environments than unsuccessful individuals and understanding the extent and causes of these differences can be important in estimating the demographic consequences of particular environmental changes.

Fifth, individual-based studies that extend over multiple cohorts provide opportunities for repeated measurement of the strength and direction of selection [40]. In many populations, the strength and (less commonly) the direction of selection varies between years and prolonged time series are invaluable for exploring the effects of demographic factors such as population density [41,42] or environmental variation on selection (e.g. [43–45].

Finally, individual-based data that extend over several generations have made possible studies of the quantitative genetics of phenotypic traits in wild populations. Estimates of the genetic variance for traits, and the genetic covariances between them, reveal the evolutionary potential of characters, and the extent to which this is constrained or amplified by links to other characters [46,47]. In the last decade, the application of powerful statistical techniques derived from animal breeding that utilise repeated observations and multi-generational pedigrees has greatly expanded the scope of our understanding of genetics of phenotypic characters in natural populations [47].

Each of these six properties of individual based studies has played an important part in contributing to recent developments in ecology and evolutionary biology. In the following sections we briefly describe six topics in which advances in knowledge over the last thirty years have depended on the availability of long-term, individual-based studies and on one or more of these properties.

Development and ageing

An understanding of age-related changes in survival and breeding success is of central importance both in research on population ecology and in evolutionary biology. Whereas a wide range of studies have been able to document changes in reproductive success and survival over the first

Box 1. Long-term, individual-based field studies of birds and mammals

The first long-term individual-based field studies of vertebrates that could recognise and monitor the life histories of large samples of individuals were of blue tits and great tits in Holland [150] and Britain [5,151] (Figure I). The same approach was subsequently extended to studies of other passerine birds [152–154], seabirds [155], waders [156,157], waterfowl [148,158] and raptors [159,160]. Longitudinal field studies of non-human mammals (Figure II) started in the late 1950s and early 1960s. Many of the first long term studies of mammals were of primates [161–163] but a similar approach was soon extended to studies of ungulates and other large herbivores [163–166], carnivores [167,168] and rodents [169,170] and later to cetaceans [171,172], bats [173,174] and marsupials [175].

Most early studies of birds followed the lead of Kluijver and Lack and used records of individual life histories to extend research on population dynamics and demography. Individuals were normally recognised from leg rings and were rarely habituated to close observation. In contrast, many of the early individual-based studies of mammals focused on describing and investigating the structure of societies and the social processes that maintained them. To collect relevant data for these studies, their subjects needed to be habituated to close observation and this typically restricted the number of groups or individuals that could be monitored. As field studies developed, these contrasts have disappeared. Long-term individual-based studies of birds and mammals are now commonly used to explore the costs and benefits of different phenotypic traits or behavioural strategies. An increasing number of studies of birds are exploring the structure of social groups and the development of social relationships between individuals [176]. Like studies of mammals, some now rely on habituating individuals to close observation and on recognition using natural markings. In addition, some studies of social birds have habituated individuals to close observation to a point at which it is possible to weigh them repeatedly. Conversely, several field studies of mammals now monitor multiple groups and several hundred individuals, marking individuals with tags, dye-marks or transponders. As sample sizes have increased, the objectives of studies have broadened and individual-based research programmes are now commonly used to investigate the dynamics and demography of populations.

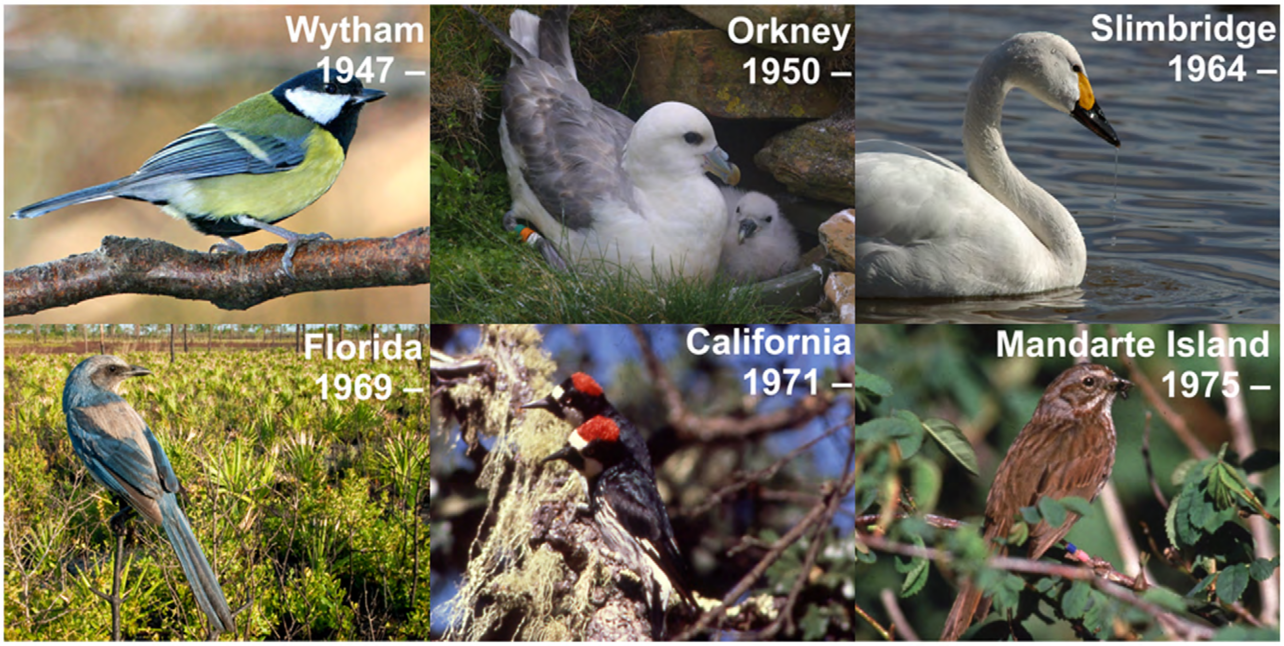

Figure I. A selection of birds that are the subject of continuing long-term, individual-based field studies: **(a)** great tit (credit Joe Tobias); **(b)** fulmar (credit Paul Thompson); **(c)** Bewick's swan (credit Paul Marshall); **(d)** Florida scrubjay (credit Reed Bowman); **(e)** acorn woodpeckers (credit Ron Mumme); **(f)** song sparrow (credit Lukas Keller). For each image, the date shows the beginning of long-term data collection at the site indicated.

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Figure II. A selection of mammals that are the subject of continuing long-term, individual-based field studies: **(a)** chimpanzee (credit Ian Gilby); **(b)** yellow-bellied marmot (credit Kenneth Armitage); **(c)** African lion (credit Craig Packer); **(d)** savannah baboon (credit Jeanne Altmann); **(e)** bighorn sheep (Fanie Pelletier); **(f)** red deer (credit Tim Clutton-Brock).

half of the lifespan, accurate descriptions of senescence in natural populations have only recently become available, especially in short-lived organisms in which few individuals survive to an age when breeding success and survival begin to decline. A wide range of studies of natural populations now show that age-related declines in survival and breeding success are widespread both in short- and long-lived species [8,48,49] and that fluctuations in age structure can generate substantial variation in mortality and population size [20]. Detailed studies of large samples of individual life histories have also made it possible to compare the rate at which different components of fitness change over the lifespan [50] and to explore the causes of individual differences in rates of senescence [51,52]. For example, recent research on birds and mammals has demonstrated the extent to which early growth and reproductive history affect age-related changes in survival [28,53,54] and fecundity [55], whereas other studies have shown that rates of ageing can be influenced by genes and maternal age when an individual is born [56–59].

Accurate measures of age-related changes in natural populations have also advanced our understanding of variation in ageing rates between species. For example, across a wide range of species, life expectancy increases as the risk of extrinsic mortality declines [48,60]. Similarly, recent studies of eusocial species, in which breeding females are provisioned by non-breeding helpers (and so are at little risk of extrinsic mortality), have shown that breeding females have unusually extended lifespans, which in some species are more than an order of magnitude longer than those of non-breeders [61,62]. They have also shed new light on the evolution of sex differences in ageing. Earlier and more rapid rates of ageing in males compared to females appear to be related to variation in the relative reproductive tenure of males and females and are characteristic of polygynous species in which mating competition constrains the length of effective reproductive lifespans in males. In contrast, sex differences in ageing are small or absent in monogamous species in which the reproductive lifespans of males and females are of similar duration [63].

Reproductive ecology and the evolution of life histories

One of the most fundamental contributions of individual-based field studies has been to understanding the extent and causes of variation in breeding success in both sexes. In many animals (and especially in long-lived iteroparous species), individual differences in breeding success are large in both sexes [25,38]. One important consequence of these differences (which has implications both for population dynamics and for the genetic structure of populations) is that a high proportion of recruits are produced by a relatively small proportion of adults [38,39,64,65]. Investigating the causes of individual differences in breeding success remains a fundamental topic of research in animal ecology. In some cases, fluctuations in the environment are key: for example, in red deer, cold weather during the last two months of gestation depresses food availability and is associated with low birth weights, which in turn affect subsequent survival and breeding success, generating marked differences in reproductive performance between cohorts born in successive years [29]. In other cases, differences in breeding success appear to be caused by variation in genotype or genotype by environment interactions. For example, inbred individuals often survive less well as juveniles and show reduced reproductive performance throughout their lives, but the extent to which inbreeding affects survival and breeding success varies with environ-

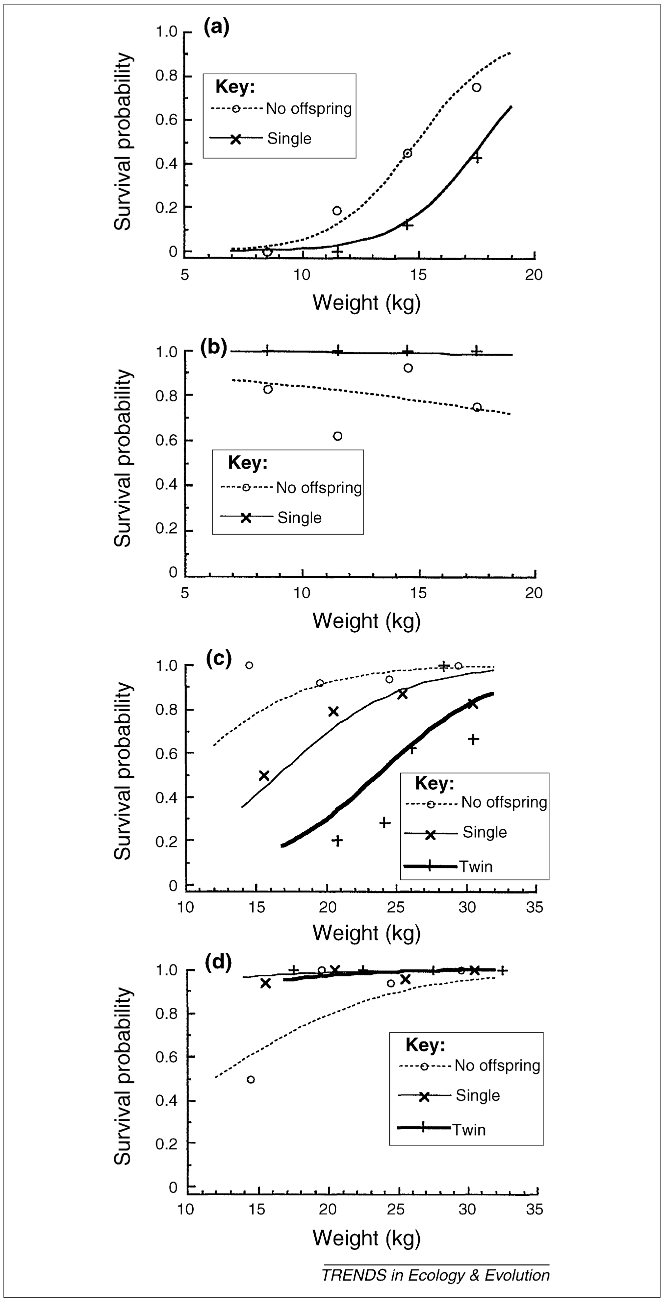

Figure 2. Effects of breeding on overwinter survival for female Soay sheep of different weight on St Kilda; **(a)** juveniles in high density years; **(b)** juveniles in low density years; **(c)** mature ewes in high density years; **(d)** mature ewes in low density years. Symbols show the proportion of animals in different categories that survived [74]. (Body weight measured in august). Reproduced from *Journal of Animal Ecology*.

mental conditions [66,67]. As in many areas of ecology, one challenge is to understand the relative importance of deterministic and stochastic processes in generating individual differences in reproductive success [68,69]. Recent models of stage-structured life history variation [70,71] have concluded that most life history variation could be stochastic in origin, providing a provocative perspective that contrasts with empirical evidence that fixed differences between individuals are widespread and are closely associated with variation in genotype and phenotype [72].

Studies of individual life histories in natural populations provide the basis for estimating the form and magnitude of trade-offs between different fitness components, the relative cost of different strategies and the extent to which they vary with ecological conditions and between different categories of individuals. Empirical studies show that the costs of breeding vary widely and that it is important to recognise these differences to understand the evolution of life-history parameters. For example, in Soay sheep, individuals commonly conceive for the first time either in their first or their second year of life [73]. In years when population density is high, females that conceive in their first year commonly die in late winter, especially if they are relatively light, whereas individuals that fail to breed show much higher rates of survival [74] (Figure 2). In contrast, in years when population density is relatively low, individuals that fail to breed show lower survival than breeders. Among mature ewes, too, the production of offspring depresses survival of light mothers in years when population density is high but has little effect in years when density is low. In both age categories, females that fail to breed show lower survival than successful breeders in low density years, presumably because they are of lower phenotypic quality or suffer from parasites or disease.

Sex allocation and sex ratio variation

Individual-based studies have also been pivotal in understanding the way in which parents allocate resources to sons and daughters. Early studies of mammals showed that sons suckle more frequently than daughters and that mothers that have raised sons pay higher costs in terms of elevated mortality and depressed future repro-

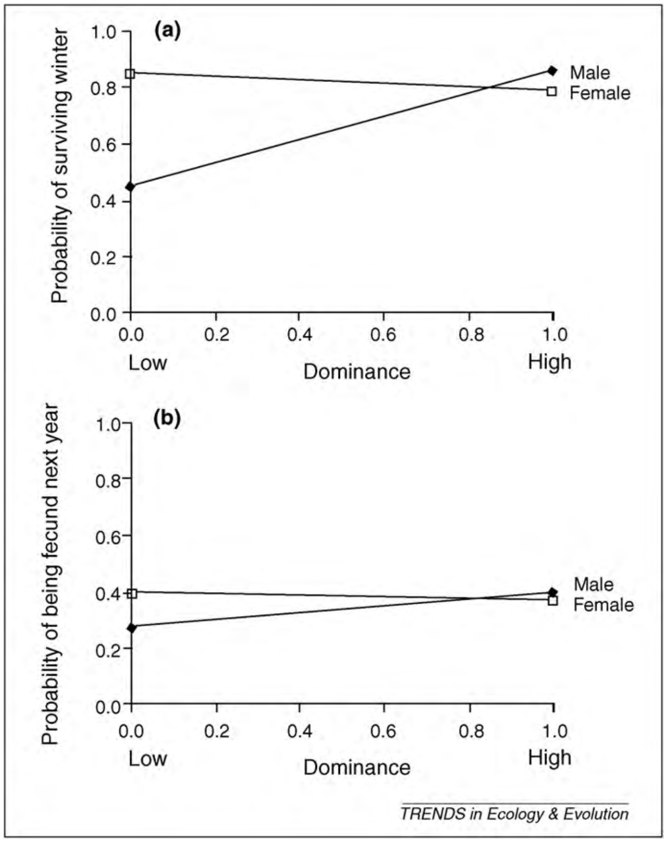

Figure 3. Costs of rearing sons and daughters of female red deer of varying status (from [77]). Figure shows the probability that dominant and subordinate mothers that have reared sons versus daughters will **(a)** survive the next winter **(b)** breed again the following year. Reproduced from *Nature*.

duction [75], confirming theoretical predictions that parents might be expected to invest more heavily in sons than in daughters in polygynous animals [76]. These effects vary with maternal rank and only subordinate mothers suffer additional fitness costs from raising sons [77] (Figure 3). Related studies have shown that differential sex allocation can also affect the development of sibs. For example, in Soay sheep, the birth weights of female lambs born with a male twin are lower than those of females born with a female co-twin [78]. Similar effects have subsequently been shown to occur in humans. For example, in some pre-industrial human populations, female twins born with male co-twins show lower fitness than females born with female co-twins [79,80].

Evidence of contrasts in the costs of raising sons and daughters stimulated studies to investigate how the relative fitness of sons and daughters vary with parental characteristics and whether individuals adjust the sex ratio of their progeny in relation to these differences. For example, in red deer, maternal dominance affects the lifetime breeding success of sons to a greater extent than that of daughters and, in low density populations, dominant mothers bias the sex ratio of progeny towards males [81–83]. Similarly, individual female Seychelles warblers adjust the sex ratio of their offspring in relation to the sex-specific payoffs, which are dependent on the quality of the environment [84]. The association between individual variation and the sex ratio is still controversial, but evidence from long-term studies, both in the form of key empirical tests, and meta-analyses across a wide range of studies, have begun to establish the conditions under which sex ratio variation at the individual level is likely to evolve [85–87].

Structure and dynamics of social groups

Long-term individual-based studies have played a central role in documenting the structure of animal societies and the costs and benefits of social relationships. One of their most important contributions has been to provide detailed measures of the frequency and distribution of dispersal, which often has important effects on the dynamics of populations [88,89] and is usually difficult to measure unless individuals can be recognised and their movements monitored. In many animals there are pronounced sex differences both in the probability of dispersal and dispersal distance [90–92], which differ between species and affect both the kinship structure of groups and the incidence of cooperation and competition between their members [32,35]. For example, in many group-living mammals, females commonly remain in their natal group and often cooperate with each other, whereas males typically disperse to breed, so that males belonging to the same group are seldom closely related and cooperation is seldom as highly developed as in females [32,90,93]. In contrast, in many group-living birds, males more commonly remain and breed in their natal group than females and cooperation tends to be more highly developed among males than females [32,90]. Several different explanations of these differences have been suggested [92], but one important factor is the probability that females will reach sexual maturity in a group in which their father is the resident dominant male [32,94]. Inbreeding with close relatives commonly has substantial costs to survival or reproductive success [66,95] and in cases in which females reach breeding age in a group in which their father or brothers are reproductively active, they commonly either delay sexual maturity, select other mating partners or disperse [96–99].

Individual-based studies have also explored the structure of social relationships and their effects on breeding success and survival. Some of the first studies of animal social behaviour identified the presence of consistent differences in dominance status between males and showed that, relative to subordinates, dominants usually achieved enhanced access to mates and increased reproductive success, although this is not invariably the case [100,101]. In species in which individuals compete alone, contrasts in rank are commonly associated with variation in individual fighting success, which is often positively related to body size and condition as well as to early development [102,103]. In contrast, in those species in which individuals support each other in social interactions, individual differences in social rank and breeding success are commonly affected by the strength and extent of social relationships between individuals and their allies or supporters [104,105].

More recently, studies that have been able to document the life histories of females have shown that here too differences in rank are often positively correlated with measures of breeding success [106,107] and are commonly affected by social relationships with other group members. For example, field studies of baboons show that the breeding success of females is often positively correlated with the numbers of their matrilineal relatives in their group and that individual differences in breeding success are affected by the total number of individuals (including non-relatives as well as relatives) that they interact with on a regular basis [33]. Recent studies of social interactions have now moved beyond the analysis of dyadic interactions, using network analysis to describe the structure of interactions between group members [108,109], and this approach is likely to be widely used in future. These studies show that individuals vary widely and consistently in their social connections with other group members and that individual differences in these connections commonly affect access to resources and the costs of social interactions [110] and have important consequences for health and reproductive success [111].

Individual-based studies have also played a crucial role in exploring the evolution of cooperative societies and eusocial societies in which group members cooperate to feed and guard young other than their own. Extensive and costly cooperation of this kind is almost entirely restricted to species living in stable groups consisting of close relatives [112–114] and is commonly associated with the physiological suppression of reproduction in helpers [115]. One important line of research into the evolution of these systems involves exploring the evolution of contrasts in the distribution of reproduction among group members [116,117]. Another involves investigating the factors that affect individual differences in contributions to cooperative activities: these are often large and are closely related to variation in the condition of helpers as well as to the probability that they will be able to breed themselves [118]. In both cases, studies rely on protracted monitoring of the behaviour and life histories of individuals.

Quantitative genetics in wild populations

Understanding the relative roles of genes and the environment is fundamental to our understanding of what phenotypic traits are, how they are likely to behave in response to selection and how changes in the global environment are likely to affect populations and communities [119]. Quantitative genetics has traditionally been the preserve of plant breeders, or those working with animals in captivity. This is largely because estimating genetic effects with precision not only needs information about the relatedness among individuals, but also needs very large samples, because the effects are often weak and highly modified by environmental variation. In recent years, long-term studies of wild animals have reached the level of maturity in terms of the number of individuals and generations available to make possible the application of flexible analytical tools from the animal breeding field [47,120] and this has injected a more explicitly evolutionary focus into work on the causes and consequences of variation in fitness and fitness-related traits. For example, several recent studies have been able to assess the cost of inbreeding in natural populations and to explore the factors affecting its incidence (Figure 4).

Quantitative genetic approaches are now commonly used to estimate the genetic variances of traits and the genetic covariances between them, providing important insights into the extent to which populations are free to evolve in response to selection, and making it possible to test specific evolutionary hypotheses. Multiple studies have confirmed that there are consistent relationships between the strength of selection on a trait and its heritability (lower for traits under stronger selection) and additive genetic variance (the opposite pattern) [121–125]. Since heritability is the ratio of additive genetic variance to phenotypic variance, this implies that traits subject to stronger selection are subject to relatively greater degrees of environmental variation. A single trait in a given population might show variable extents of genetic variation with environment [44], or with age [126] and this might be important for the trait's evolutionary dynamics. For example, in Soay sheep, heritability of birth weight is lowest in years when selection on birth weight is strongest, suggesting a constraint on any evolutionary response [127]. Studies of the covariance between traits are also crucial for understanding their evolutionary dynamics. For example, in Soay sheep the genetic covariance between horn size and lifetime reproductive success changes sign across a key environmental gradient, suggesting how variation in horn size is maintained [128]. In mute swans, the genetic covariance between age of first breeding and age at last breeding is negative, providing support for antagonistic pleiotropy models of the evolution of senescence [56].

These studies of quantitative genetics in wild populations are likely to be the first wave of a series of studies, which will make increasing use of genetic marker-derived information to aid the mapping of phenotypes to genes [129–131], and, ultimately, the identification of specific loci underpinning individual variation in populations. This is a fast-moving area in which advances in technology are driving rapid increases in the scale and ease with which genetic information can be obtained, but it remains the case that good quality phenotypic data, for animals spanning a range of generations, will continue to be invaluable and the availability of these data could limit the rate of progress. By contrast, one very welcome development is that genetic tools open up a wider range of possibilities in terms of the types of organisms and mating systems that can be studied effectively, and for which longitudinal studies of marked populations become feasible [132].

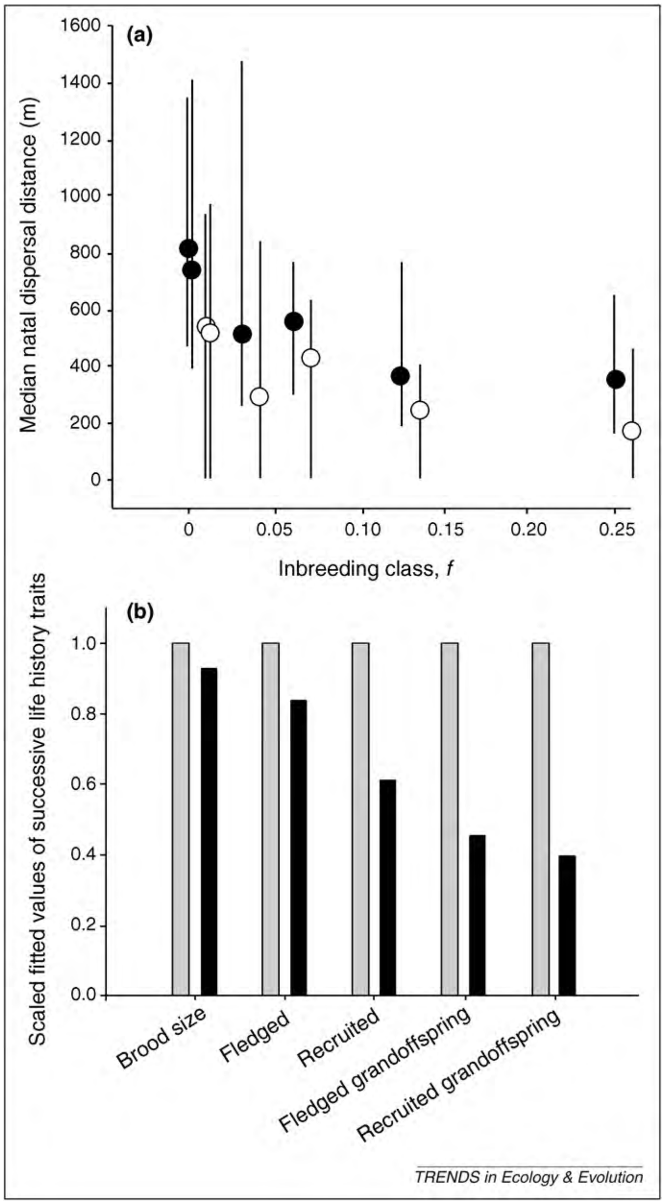

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Figure 4. Causes of inbreeding, and its long-term fitness consequences for individual great tits. **(a)** Natal dispersal distances (means and interquartile ranges) for great tits (open symbols males, closed symbols females) that mated with partners related to them to different degrees (from [149]), Reproduced from *Proceedings of the Royal Society London B*; **(b)** Cumulative effect of inbreeding on successive life history stages in a wild population of great tits. Pale bars show values for offspring resulting from outbred matings ($f_{(ij)} = 0.0$, scales to 1.0); black bars show values for offspring resulting from inbred matings ($f_{(ij)} = 0.25$) (from [67]). Reproduced from *Journal of Evolutionary Biology*.

The evolution of phenotypic plasticity

Repeated observations of individuals, and the ability to link observations across all stages of an animal's life history, are also important prerequisites for understanding the ability of individuals to produce flexible phenotypes

Box 2. Changes in phenotype with time

Phenotypic change associated with temporal changes in the environment (including those caused by climate change or other anthropogenic factors) can arise via a number of mechanisms and it is important to distinguish between them in order to access the permanence of changes and their likely consequences (Figure I). Currently, we have little understanding of the extent to which these changes reflect evolutionary change within populations [177], but data from longitudinal studies of individuals offer a number of methods to do so:

(i) Regression of mean estimated breeding value on time, to test for a change in the additive genetic breeding value over time, which would be evidence for evolution (see [178] for cautionary notes relating to this approach).
(ii) Comparison of the average phenotypic plasticity along a given environmental gradient (short, continuous lines) with the population mean response across the same gradient (long, dashed line). If the average within-individual plasticity is the same as the rate of response at the population level, this suggests that the entire population response can be accounted for by phenotypic plasticity.
(iii) The rate of phenotypic change over time can be estimated in terms of standard deviations per generation; if the heritability of the trait is known, or can be assumed, this yields a prediction of the average strength of selection needed to produce a change of this magnitude.
(iv) Finally, the rate of phenotypic change per generation can be compared with the theoretical maximum (R_{max}) sustainable within populations.

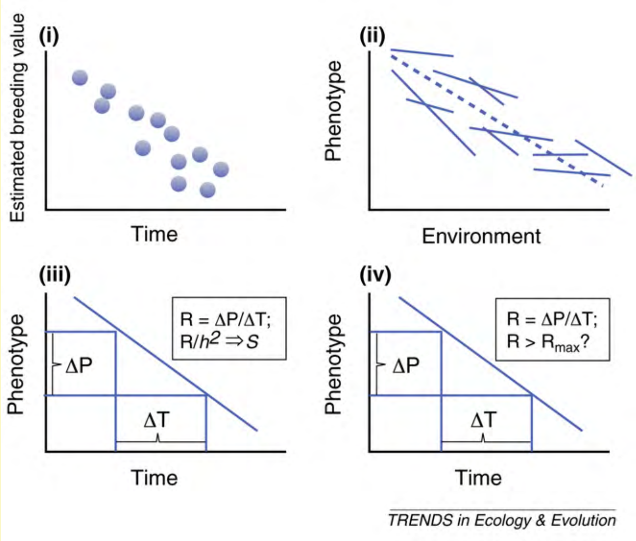

Figure I. Techniques for assessing the evidence for evolutionary responses to environmental change within populations. Reproduced with permission from *Effects of Climate Change on Birds*, Oxford University Press [179].

in response to both internal and external aspects of their environment. An increasing number of studies have documented persistent effects of natal conditions on life histories in birds and mammals, including humans [133–137] (although they are not ubiquitous [135,138]). There is now a need to understand the mechanistic basis of these effects [139], and whether they represent adaptive responses to differing environments, or are a consequence of energetic constraints on development [140,141]. Effects of this type are of particular interest because it may provide a simple mechanism for environmental effects to be transmitted across generations, and could contribute to long-term differences in population dynamics across environments [142], generating positive feedback loops that cause increased differentiation among individuals.

Phenotypic plasticity often provides a key means by which a match between the phenotype and the environment is achieved, especially for iteroparous organisms [143]. Repeated observations of individuals facilitate the characterisation of plastic responses, and analytical frameworks have recently been developed to partition population-level variation into within- and between- individual components, and to partition the latter into components that have genetic or environmental sources [144,145]. As yet, our understanding of the causes of variation in plasticity within populations is rudimentary. However, preliminary work suggests that the extent of plasticity in response to the same environmental cue can vary across populations of the same species [146] and that variation in maternal conditions can lead to differences in the average degree of plasticity in offspring size [147]. Exploration of phenotypic plasticity in natural populations has also been carried out in the context of understanding the mechanisms underlying responses to climate change, and provides a framework for distinguishing among potential mechanisms for change. Distinctions of this kind can only be achieved effectively with longitudinal studies of marked individuals (Box 2).

Challenges facing long-term individual based studies

Although they offer important insights into ecological and evolutionary pressures, long-term individual-based studies are often complicated to run and difficult to maintain [26]. Many of them (especially studies of the larger mammals) have to be carried out in isolated areas and face logistical problems ranging from access to regular supplies to political instability and direct threats to resident scientists. Researchers based in national parks and natural reserves are often subject to restrictions on their activities and many conservation authorities have become increasingly sceptical of the value of long-term research unless it provides direct guidance to management. Most long-term studies necessarily involve the collection of data by many individuals and so maintaining consistency and quality is seldom easy. In addition, the need to monitor the full life histories of large samples of individuals under consistent conditions is often at odds with the need to test specific hypotheses through controlled experiments which affect the life histories of individuals, the consistency of demographic records and the ability to monitor the consequences of long term environmental changes.

Of all the obstacles faced by long-term studies, the greatest single problem is the difficulty of maintaining funding without interruptions. As time passes, grant committees require continuing evidence that studies are remaining productive and are continuing to break new ground. So just how productive are long-term studies and how does their output change with time? Because we could find no relevant analyses, we carried out a survey

Box 3. The output of long-term, individual-based field studies

Our survey of long-term field studies based in the UK included publication records for fifty-one long-term (>10 years), individual-based studies of which the longest had been running for more than fifty years (Figure Ia). The sample included most of the well known long-term studies in Britain: great tits and blue tits, pied flycatchers, mute swans, Bewick's swans, fulmars and kittiwakes, red deer and Soay sheep. Almost all of these studies were reasonably productive, but a quarter of them were exceptional, producing multiple publications each year and large numbers over the total period they had been running (Figure Ib). Most of these have been able to document the life histories of large numbers of individuals and now involve scientists from several different universities or institutes with complementary expertise, who share access to a common data-base containing the life histories of large numbers of individuals.

Analysis of the publication trajectories of the studies in our sample shows that, in general, the longest running studies are the most productive. In the majority of cases, the first publications only appear after studies have been running for several years. Subsequently, annual rates of publication increase rapidly and continue to do so for at least two decades (Figure Ic). In addition, the probability that studies will generate at least one paper per year in a high impact journal (defined for the purposes of this study as a paper in *Science*, *Nature*, *PNAS* or *Current Biology*) increases rapidly (Figure Id), suggesting that the originality of the work increases with the duration of studies.

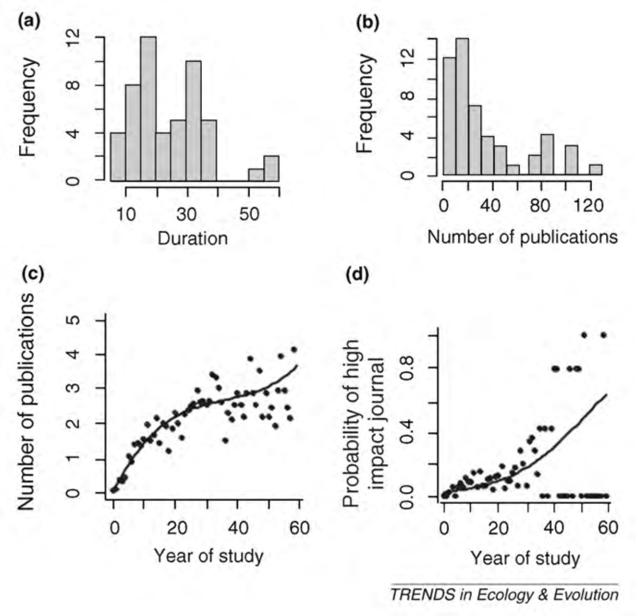

Figure I. Output of 51 long-term, individual based studies based in the UK **(a)** frequency of studies of different duration; **(b)** total publications per study; **(c)** publications per year of study; **(d)** probability of producing a paper in *Science*, *Nature*, *PNAS* or *Current Biology*/per year.

of the publication record of long-term animal field studies in the UK in collaboration with Kelly Moyes (Box 3).

Our analysis showed that a relatively small number of high quality, long-term, individual-based studies are responsible for a disproportionate number of publications in organismal biology and, especially, for publications in journals with the highest impact factors. The reason for their high productivity is not difficult to identify. Access to large numbers of recognisable individuals with known life histories spanning many years provides the possibility of asking (and answering) a wide range of novel questions that are otherwise inaccessible. This then paves the way for statistical analysis or experiments that isolate the effects of particular parameters, which could not be feasibly performed on samples of unknown individuals. In addition, long-term individual based studies offer opportunities to test assumptions used in other studies of ecological and evolutionary processes in other species in which similar data are unavailable. And, because of the quality, extent and sophistication of the data, a high proportion of organismal biologists that win senior post-doctoral jobs or lectureships have worked on one of them at some stage of their careers and so the same studies make an important contribution to training ecologists and evolutionary biologists

As research in organismal biology develops and understanding the biological consequences of environmental change becomes increasingly necessary, the importance of long-term studies providing precise demographic data and long runs of reliable records of individual life histories is likely to grow. However, the usual structure of research funding based on three-year grants is poorly suited to maintaining them. Even if grant applications are carefully structured and their aims are novel, applications are bound to fail at some stage, generating interruptions in the continuity of data that affect records of the life histories of a large proportion of individuals in the population and, in some cases, causing long-term studies to be abandoned. Finding a better way of supporting long-term ecological research that helps to maintain long-term studies but does not unfairly advantage them should be one of the concerns of institutions funding ecology and evolutionary biology.

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