

## Review



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# Leveraging big data to uncover the eco-evolutionary factors shaping behavioural development

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Mapping the eco-evolutionary factors shaping the development of animals' behavioural phenotypes remains a great challenge. Recent advances in 'big behavioural data' research—the high-resolution tracking of individuals and the harnessing of that data with powerful analytical tools—have vastly improved our ability to measure and model developing behavioural phenotypes. Applied to the study of behavioural ontogeny, the unfolding of whole behavioural repertoires can be mapped in unprecedented detail with relative ease. This overcomes long-standing experimental bottlenecks and heralds a surge of studies that more finely define and explore behavioural–experiential trajectories across development. In this review, we first provide a brief guide to state-of-the-art approaches that allow the collection and analysis of high-resolution behavioural data across development. We then outline how such approaches can be used to address key issues regarding the ecological and evolutionary factors shaping behavioural development: developmental feedbacks between behaviour and underlying states, early life effects and behavioural transitions, and information integration across development.

## 1. Background

During the last decade, the rapid emergence of 'big behavioural data' research—the high-resolution tracking of individuals and the harnessing of that data with powerful machine learning techniques [1–6]—has spurred major advances in fields as diverse as behavioural genomics and transcriptomics [7–9], behavioural neuroscience [10–15], collective decision-making [16–19] and movement ecology [20–23]. Huge untapped potential remains, however, in applying big data approaches to understand the development of behaviour. In sharp contrast to previous data-limited approaches where only subsets of animals' developmental trajectories are measured, big behavioural data research allows near-continuous monitoring of animals throughout their entire (or substantial parts of) development. We believe that this innovation, paired with timely advancements in computation, data storage, and tailored analytical tools, represents a watershed moment for understanding the ecology and evolution of behavioural development.

In our review, we begin (§2) by briefly reviewing the state-of-the-art approaches that allow the collection and analysis of behavioural data at increasing resolution. Then, we discuss in detail (§3) how these innovations in measuring and modelling behaviour can be productively applied to fundamental open questions regarding the rules governing the unfolding of behaviour: mapping the

nature of developmental feedbacks between behaviour and underlying states, understanding early-life effects and behavioural transitions across development, and understanding information integration across development. Big behavioural data have greatly expanded the empirical toolkit with which to investigate these fundamental issues in behavioural development, and they have also spurred a new generation of conceptual models of behaviour. Throughout, we focus on the links between contemporary and potential future empirical advances and the set of theory and technical models that this new wealth of data can inform and test. Indeed, many of the state-of-the-art methods in behavioural analysis that we review are increasingly simple to use and ready to deploy, but their application to existing theory in behavioural development is largely unrealized; quick progress in this area is thus achievable, as we will outline. In sum, we believe that this mutual feedback between new data sources and novel theory will generate major new insights into one of the foundational elements of the study of behaviour, behavioural ontogeny.

## 2. New methods, measures and means of defining behaviour

One inherent difficulty with measuring the ontogeny of most traits—behaviour among them—is that, for many organisms, these traits often take considerable time to fully develop. Historically, behavioural researchers have tried to circumvent this issue in several ways (table 1): by limiting the period in development over which a trait is measured; by measuring a trait during relatively short periods during development interspersed by larger intervals of time without measurements; by manipulating early-life conditions and investigating the consequences later in life; and/or by adopting comparative approaches across individuals of different ages. These methods, while providing targeted information about certain periods during development or coarse-grained information about the arc of development, may miss critical time windows and complex nonlinearities in behavioural development, thereby hampering our ability to gain a fuller understanding of the factors shaping behavioural development. Additionally, constraints on data collection have also meant that most studies focus on the development of one or a few behavioural traits and thus miss out on quantifying biologically meaningful correlations in developmental time series of suites of traits.

Whereas collecting highly time-resolved data on behaviour through the entire course of development was once often prohibited by daunting logistics and limits on time and effort, the advent of sophisticated automated tracking technology, more advanced data storage infrastructure, and a host of powerful, data-hungry analytical tools can produce and parse these datasets with relatively low cost in terms of both person-hours and monetary investment [10,41,42]. We are now at a critical juncture where early studies have proven the worth of these new technologies for quantifying and conceptualizing behaviour in new ways [10,43–46], but where heretofore surprisingly limited consideration has been paid to the application of these tools to behavioural development. For the remainder of this section, we focus on recent innovations in both the measuring and modelling of behaviour that lay the foundation for the application of these technologies to answer major open questions in behavioural development.


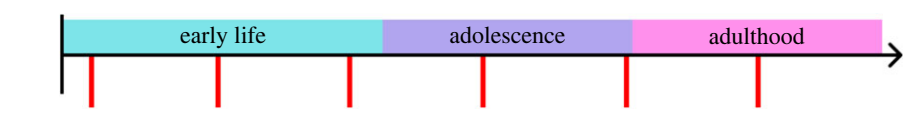
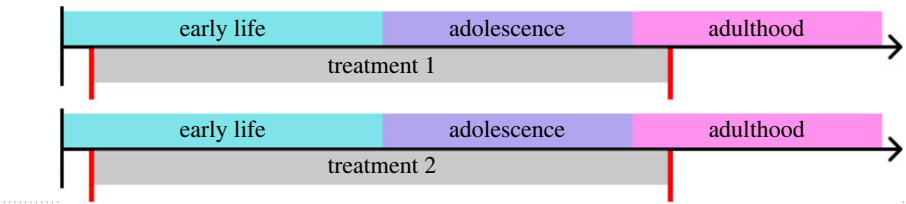
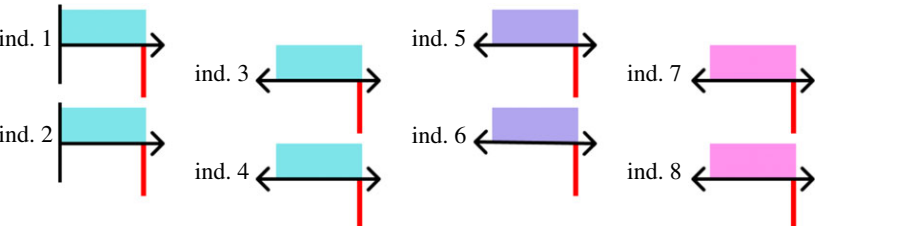
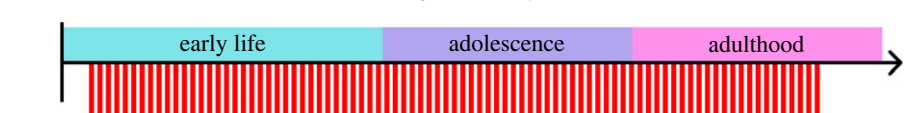
### (a) Measurement innovations

Behavioural tracking technology has come a long way in the last decade, with sub-second temporal resolution in movement data now being standard for many automated real-time trackers. Such datasets, often as simple as a time series of two- or three-dimensional coordinate points in space, are commonly obtained via GPS devices, PIT tags, or video tracking, and numerous tracking software automate the process of converting coordinate point data into behavioural metrics such as activity rates, space use, velocity, etc. [2,6,47–50]. Crucially, many of these tools are specifically designed for keeping track of individuals through time, even when observed in groups, allowing behavioural patterns of many individuals to be tracked simultaneously [6,48,49]. Furthermore, rapid advances are being made in the identification and tracking of postural movements of body segments, allowing studies of fine motor development of social interactions, mating displays, resource manipulation, etc. [2,51]. Such approaches have vastly increased both the temporal resolution and overall duration of data that can be collected, allowing animals to be tracked throughout development with minimal intervention. Tracking technology is not just limited to tracking animal behaviour during development: some of the greatest promise lies in pairing high-resolution behavioural tracking data with complementary, non-behavioural data types with similar resolution. For instance, high-resolution behavioural data coupled with other high-throughput data sources have provided insight into both the neurological [14,52] and transcriptomic correlates of behaviour [8]. Internal state variables such as body condition can be estimated directly from video frames in the case of video tracking [53]. High-resolution physiological data can be obtained from a quickly expanding array of non-invasive biologging tools [54,55], such as heart rate monitors [56,57] or thermal imaging [58–60], and may help infer stress levels, respiration rate or energetic state when coupled with behavioural data. Other approaches use both supervised and unsupervised machine learning methods to infer underlying internal state variables from high-resolution behavioural tracking data themselves [61–64]. We believe there is also tremendous value in the simultaneous tracking of salient environmental variables and behaviour [65–67], allowing researchers to map detailed behavioural–experiential trajectories (i.e. interactions between behaviours and the sequence of experiences that result from interacting with the environment) and track environmental drivers of behaviour throughout development, getting us a step closer to understanding the ecological forces shaping behavioural development.

### (b) Data-driven definitions of behavioural axes

Behavioural biologists have long wrestled with how to identify and classify behavioural ‘traits’ [68,69], and while novel methods of measuring and conceptualizing behaviour may not be a panacea, they offer progress. Equipped with highly resolved behavioural time series over ontogeny, researchers have a quickly growing toolset of analytical techniques that permit, for example, high-throughput auto-labelling of observer-defined behaviours [70], unsupervised learning of new behavioural classes, detection of hierarchical sub-structure in behaviour, or modelling of behavioural transition rates across a wide range of timescales [10,12,42,71].

**Table 1.** A stylized overview of the main methods used to study the development of behaviour, including near-continuous behavioural measurements throughout development, that advances in tracking, computational and analytical tools have recently made possible.

methods of quantifying behavioural development	example references
<p>(1) concentrated measurements early in life</p> 	[24,25]
<p>(2) periodic measurements throughout development</p> 	[26–30]
<p>(3) experimental manipulation early in life, behavioural measurements before/after</p> 	[31–35]
<p>(4) comparative approach across individuals of different ages</p> 	[29,36–38]
<p>(5) near-continuous behavioural measurements throughout development</p> 	[39,40]

Big behavioural datasets are large and often inherently multi-dimensional, and while researchers may opt for dramatically reducing the dimensionality of these datasets by, for instance, calculating simple behavioural metrics directly from raw data (e.g. activity rates, velocity, position in relation to focal point or social partner, etc.), a range of tools can now be applied that retain the high dimensionality of these datasets to the degree that it is informative, thus moving a step closer to quantifying the development of integrated behavioural repertoires. While the specific toolkit in parsing big behavioural datasets will vary depending on the dataset and the questions to be answered, a common challenge among most analyses is reducing collinearities in the data structure while maintaining informative variation and interpretability. This task—determining the salient axes over which behaviours vary through ontogeny—sets the stage for then delimiting specific sets of related behaviours (also known as behavioural ‘classes’ or ‘clusters’) along these axes.

One of the simplest approaches for extracting behavioural axes in large, highly dimensional datasets is principal component analysis (PCA) [72]. More sophisticated techniques such as spectral analysis [73] or time frequency analysis [43,45] are specifically designed for time-series analysis and

have also been productively applied to behavioural time series as a step towards defining the axes of behavioural variation across development. The important point is that, rather than researchers pre-defining which behavioural axes are important, the primary goal of these techniques is to leverage variation in the data themselves in order to determine axes of behavioural variation among a suite of (often correlated) behavioural metrics. In a dataset of bee behaviours across their adult lifetime, for instance, PCA was applied to a set of metrics derived from tracking data (e.g. location in the hive and movement metrics such as speed and space use), allowing the authors to avoid redundancies among many potentially non-independent metrics and instead define orthogonal behavioural axes ordered by the degree to which they explained variation in the overall dataset [39]. PC axes and more complex, nonlinear dimension reduction techniques [74,75] are also highly useful as visualization tools: high-dimensional behaviour such as specific posture patterns [43,44,46,76,77], social interactions [78] or microhabitat-related behaviours [79] have all been mapped using computational approaches to defining behavioural axes. The diversity of tools in this toolset allows researchers to accommodate the many unique challenges that might arise

when, for example, behavioural covariance structures change across development (e.g. thus affecting the ‘loadings’ in a PCA), or when trade-offs between mapping ‘local’ versus ‘global’ behavioural variation are rebalanced [80].

Using statistical techniques to define the major axes of variation in behavioural time-series data has the potential to offer insights into fundamental questions about the structure and development of individual behavioural variation, that is, individuality. Traditionally, studies on behavioural individuality and animal personality have sought to describe behavioural variation along researcher-defined axes such as ‘boldness’, ‘exploration’ and ‘sociality’, a modification of the ‘Big Five’ model of personality variation imported from human psychology [81]. While this tradition is now firmly embedded in animal personality research, a steady flow of critique has questioned both the wisdom of defining traits *a priori* (e.g. whether something like ‘boldness’ or ‘exploration’ holds the same meaning across diverse species) and the methodological *status quo* of measuring behaviours along pre-defined axes (e.g. whether a certain assay actually measures ‘boldness’, ‘exploration’, etc.) [69,82–84]. Data-driven statistical approaches to defining behavioural axes have indeed been offered as alternatives to pre-defining such axes when quantifying individuality [85,86] (but see [87]), and the growing availability of high-dimensional behavioural datasets increases their appeal. Such methods may allow more comparability across periods of development, populations or even species, by first inferring the behavioural axes using data from all developmental time points/populations/species in an analysis and then asking how time points/populations/species differ across these ‘latent’ axes.

### (c) Identifying behavioural classes and quantifying transitions among classes

Once the axes of behavioural variation are identified, an important next step is delimiting how different behaviours distributed along these axes interrelate to each other, creating a ‘map’ of the structure of observed behavioural variation. Again, there are a diversity of methods to achieve this; however, one exciting set of methods, unsupervised behavioural classifiers (i.e. clustering algorithms), are increasingly being applied to big behavioural datasets as tools to define behavioural classes—groups of behavioural variables with high similarity [63,80,88,89]. Clustering, while not necessarily appropriate for all big behavioural datasets or questions, excels as a tool for dividing large, multi-dimensional behavioural data trait-spaces into interpretable subregions based on similarity, distance, or regions of high density in data space. In many cases, researchers may choose to forgo clustering: behavioural plasticity, for example, could be quantified without defining clusters and instead measuring ‘movement’ or ‘behavioural entropy’ in a multi-dimensional ‘behavioural space’. On the other hand, delineating clusters—or discrete groups of behaviours—may become useful when, for example, researchers are interested in understanding transition rates among distinct regions of behavioural trait-space throughout development. Used as tools to define behavioural diversity in entire behavioural repertoires, such methods are essentially a way to generate rich, data-driven ethograms.

A host of clustering algorithms has been deployed in unsupervised classification of behaviour, but many take as an input a specified and arbitrary number of clusters (i.e. behavioural

classes),  $k$ , in a multi-dimensional data space [80]. While one might treat the decision about the magnitude of  $k$  as an optimization problem, many of the behavioural trait-spaces that are created with high-dimensional, dense behavioural data may not show clear, discrete boundaries between identified clusters [39]; in such cases,  $k$  is perhaps most useful as a parameter that is actively toggled to adjust the ‘graininess’ of behavioural partitioning. Indeed, creative, flexible use of  $k$  as a free parameter enables researchers to examine the structure or ‘architecture’ of behavioural repertoires. For example, Berman *et al.* [44] showed that, as they increased the number of clusters,  $k$ , new clusters were created largely by subdividing existing clusters in two (rather than more substantially reshuffling the behavioural map); this led the researchers to conclude that observed fly behaviours were structured hierarchically, testing decades-old theory in ethology [90,91].

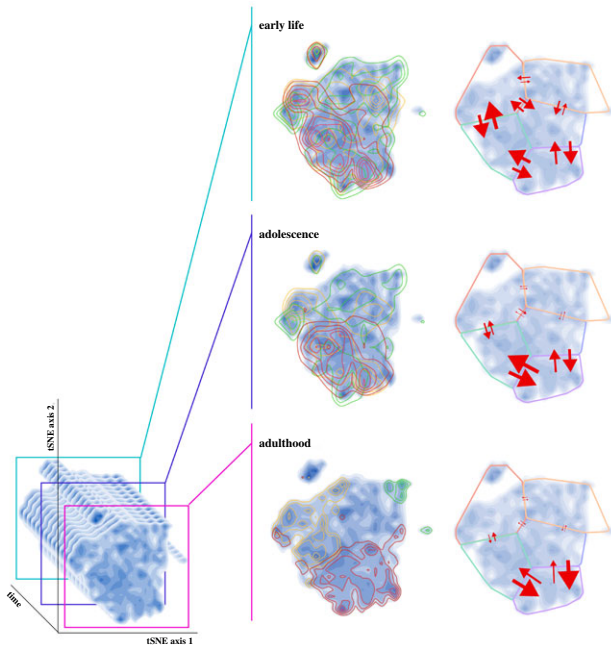
Finally, once distinct behavioural clusters/classes are defined, the transitions among these classes can be quantified. One of the simplest and most common approaches to modelling behavioural transitions is to assume that behavioural transitions follow a Markovian process. These models assume that the probabilities of transitioning to any other behavioural state (i.e. cluster) depend only on an animal’s current behaviour, rather than some sequence of behaviours that preceded the current behaviour. Common extensions of this concept are hidden Markov models (HMMs) whereby a sequence of behavioural patterns (e.g. movement) are linked to an underlying unmeasured (behavioural) state variable (e.g. a specific behavioural class such as foraging, hiding, walking and running). In this way, HMMs can be important tools in identifying behavioural modes [73,92], similar to behavioural clusters discussed earlier. Recently, HMMs have been extended to include nested latent states in order to explore hierarchical structures in behavioural modes (hierarchical hidden Markov models, HHMMs) [93,94]—an approach that is likely to be useful in high-resolution behavioural development data that can be parsed at a large range of temporal scales.

By determining the axes of behavioural variation, mapping onto these axes distinct behavioural classes or clusters, and then quantifying transitions among these classes, we can begin to ask questions that shed light on behavioural changes throughout development (figure 1): how do transitions between behaviours (i.e. clusters) change during development? Are there certain regions of this ‘behavioural map’ that are more frequently used by newborns versus adolescents versus adults? Are there certain areas of behavioural space that are only accessible to animals after a certain developmental time point? Do individuals decrease or increase in the amount of behavioural ‘space’ they use throughout their lifetime? Are individuals consistently different in how they ‘move through behavioural space’ during development? While many of these questions have been asked (and addressed) in some form previously, the degree of precision and depth with which these questions can now be addressed—not just for particular behaviours but for much of an animal’s entire movement repertoire—is unprecedented.

## 3. Using big behavioural data to uncover the principles governing behavioural development

We will now discuss how big behavioural data and the associated innovations in measuring and modelling behaviour





**Figure 1.** After dominant behavioural axes have been calculated (e.g. via PCA), multi-dimensional behavioural data for all individuals and all developmental time points can be projected onto a two-dimensional behavioural/phenotypic space (e.g. via tSNE (*t*-distributed stochastic neighbour embedding), UMAP (uniform manifold approximation and projection) or other dimension reduction tools). Individual behavioural repertoires during subsets of development can then be characterized (here with contour plots of three individuals in green, yellow and red shown only for early life, adolescence and adulthood for ease of visualization; note that high-temporal resolution allows much finer-grained analyses across many more individuals), and further quantification of individual behavioural transition rates among distinct behavioural classes/clusters can be conducted (represented for the ‘red’ individual with arrows for which size and thickness are proportional to the magnitude of transition probabilities between different behavioural clusters). In this example, individuals explore a large range of behavioural space early in development but become more constrained—and distinct from each other—as development progresses. Such a pattern of decreasing behavioural plasticity across development is a major prediction of many Bayesian models of development, and a pattern of behavioural divergence among individuals across development is consistent with behavioural niche specialization [95,96]. See [43,44] for worked examples of many of the above approaches in a non-developmental context.

discussed above can be productively applied to fundamental open questions regarding the principles governing behavioural development.

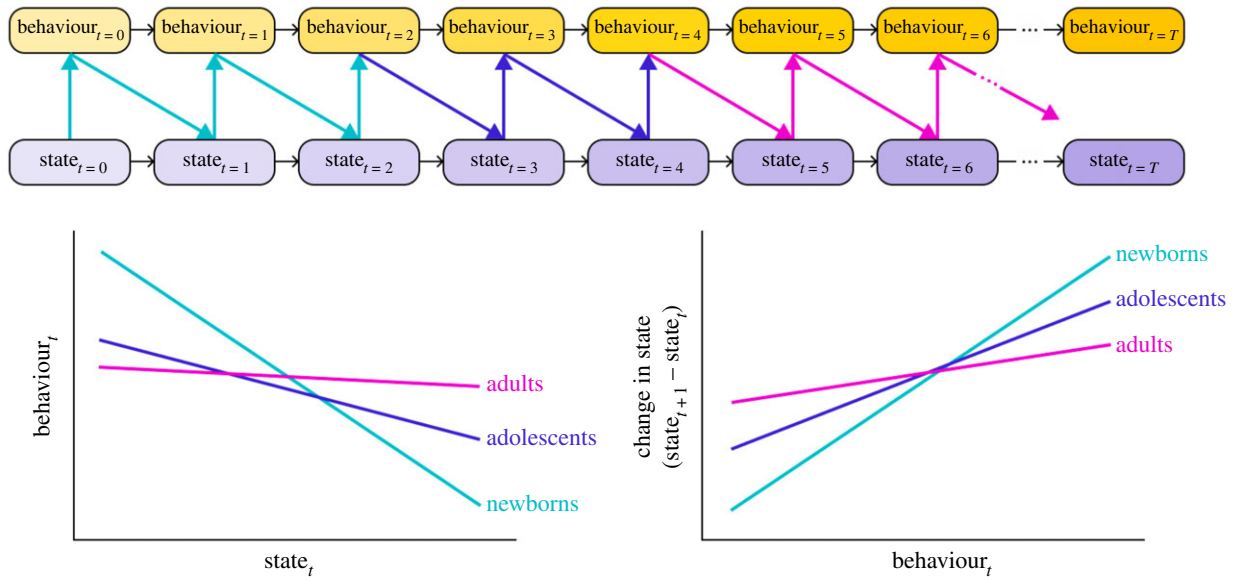
### (a) Mapping behaviour–state connections across ontogeny

Connections between behavioural decisions and an animal’s underlying state (e.g. energetic state, informational state, social rank, etc.) may play a major role in the development of behaviour: such connections can help explain the evolution and development of a large range of behaviours and states (e.g. foraging tactics [97,98], anti-predator behaviours [99–101], emotions and self-awareness [102,103], developmental adjustments in response to environmental change [104,105]). While theoretical and conceptual models employing techniques such as stochastic dynamic programming [106] have hugely facilitated the investigation of behaviour–state connections and their role in the development of adaptive

behaviour [107–112], empirical studies that simultaneously measure behaviour and state throughout development are relatively few. As discussed above (see §2*a*, ‘Measurement innovations’), behavioural tracking techniques provide a powerful way to directly measure state variables (or proxies of state variables) with as much automation as behaviour, allowing direct tests of the wealth of theory on behaviour–state connections with high-resolution behaviour and state time series across development.

One major open question is how particular types of behaviour–state connections such as dynamic feedback loops (i.e. bidirectional linkages between state and behaviour) influence developmental trajectories [113–115]. So far, of the studies that have been designed to detect behaviour–state feedbacks, conclusions on the presence and consequences of these feedbacks have been mixed [116–119]. Nevertheless, behaviour–state feedbacks are commonly cited in the literature as a major causal factor in the formation of behavioural developmental trajectories. The now possible simultaneous high-resolution tracking of both behaviour and state can allow us to (i) detect the presence of feedbacks and (ii) measure the persistence of both the strength and direction of these feedbacks across development at a much finer temporal grain. To be concrete, consider a high-resolution time series of behaviours and states, where at each point in time  $t$ ,  $B_t$  and  $S_t$  represent behavioural and state measurements, respectively (figure 2). Behaviour–state feedbacks would be evident if  $S_t$  correlated with  $B_t$  and  $B_t$  was then correlated with a change in state (i.e.  $\Delta S_t = S_{t+1} - S_t$ ) at some future point in time,  $t + 1$ . As an example, one could imagine that energetic state (e.g. fat reserves or hunger level) would affect foraging behaviour at one time point and that the intensity of any foraging behaviour would then subsequently be related to a further change in energetic state at the following time point. Furthermore, by testing for these correlations over subsets of a developmental time series, one could test for the degree to which feedbacks persist in both strength and direction throughout development. Such an investigation could test whether the slopes in the relationship between  $S_t$  and  $B_t$  and  $B_t$  and  $\Delta S_t$  vary as  $t$  increases, and whether any changes are symmetrically represented in both relationships.

One commonly cited behaviour–state feedback mechanism is the asset-protection principle [120]: if having high ‘state’ (here, residual reproductive value) makes it less likely that an individual will take risks (here, actions that are associated with increased mortality but potentially increased state benefits, e.g. foraging under predation risk), a negative feedback might be generated [121,122]. Low-state individuals would thus take more risks compared with high-state individuals, thus increasing their state and becoming less likely to take further risks. The strength of this negative feedback may be expected to change over development (figure 2). For example, prey outgrowing a dominant gape-limited predator or gradually learning how to better evade predators may represent particular ecologies that generate systematic decreases in risk—and hence the strength of the negative feedback—through a prey’s lifetime [123]. Figure 2 illustrates such a scenario where temporally high-resolution behaviour and state tracking allow us to test for the change in behaviour–state feedback strength across development: while negative feedbacks, indicated by slopes of the relationships between  $S_t$  and  $B_t$  and  $B_t$  and  $\Delta S_t$  having opposing signs, persist throughout development, the absolute



**Figure 2.** High-resolution behavioural tracking paired with similarly high-resolution tracking of state variables allow tests that detect behaviour–state feedbacks and quantify how both the strength and direction of these feedbacks change across development. In this schematic, for example, negative feedbacks between behaviour and state persist throughout development, but are stronger earlier in life (blue–green lines represent individuals in early development, purple in mid-development and magenta at maturity; note that with highly temporally resolved datasets, such an analysis could be done more continuously).

values of the slopes of these lines—and thus the strength of feedbacks—decrease through life. Thus, the ability to detect behaviour–state feedbacks and quantify how the strengths of these feedbacks change through time will afford us greater potential to map the rules governing the unfolding of developmental trajectories to the specific selective forces particular to a species' ecology.

### (b) Early-life effects and behavioural transitions

Continuous tracking of behaviour during development is particularly promising for understanding early-life effects [124,125]. Such early-life effects (e.g. parental imprinting or social experience during early life stages [126–128], the influence of early-life stressors on later behaviour [129,130], etc.) are typically studied experimentally by manipulating environmental stimuli early in life and then measuring outcomes (e.g. behaviour) later in life (table 1, example 3). The focus on early life has been particularly intense relative to other periods of animal life because (i) the developmental consequences of phenotypic adjustments made early in development may be outsized compared with those of later adjustments (e.g. the epiphenotype hypothesis [131]), (ii) animals may show greater developmental plasticity early in life [107], perhaps reflecting adaptive strategies in environments where animals gradually accrue fitness-related information from steady streams of imperfect cues [132], and (iii) early-life experiences often have long-lasting consequences for behaviour and fitness [133–136], with effects even persisting across multiple generations [137]. Despite their importance, however, the developmental routes connecting early-life experiences and their long-term outcomes often remain unmeasured and thus obscured.

Experiments based on near-continuous tracking throughout development will allow us to unravel the behavioural mechanisms that link early-life experiences to outcomes later in life. High-resolution tracking will provide both longer and more highly resolved time series of behavioural data that measure the entire developmental time course of responses

to salient early-life stressors or stimuli. Whereas previous approaches might capture gross patterns or periods of sensitivity to cues in a few key periods of development, high-throughput behavioural measurements could more closely estimate the exact 'cue–response curve' [138]. Of key interest will be the periods of life near 'switching points' in cue sensitivity when animals switch from being sensitive to cue input to being unresponsive to cues. A highly temporally resolved dataset could then address, for example, whether these switching points represent a rapid switch, which may signal a threshold-mediated response or criticality in the underlying cue–response systems [139], or a more graded change in cue sensitivity, as one might observe during many learning processes [111,140]. Furthermore, it is around these switching points that individual variation is likely to exist; differences in the timing and magnitude of cue responses to ecological factors will further our understanding of the ecological and evolutionary factors driving individual variation.

While switching points often represent relatively brief and intense periods of behavioural transition, individuals are also transitioning among behavioural states on more frequent timescales second-by-second and day-by-day. Such state-switching is another important facet of behavioural development and—as we have discussed above (see §2c, 'Identifying behavioural classes and quantifying transitions among classes')—can now be captured by high-resolution behavioural tracking. And while state-switching models that calculate transition probabilities among behavioural states have been applied to behavioural data for decades, relatively large temporal graininess has only allowed transitions between high-level behavioural categories to be modelled [141,142]. By contrast, the richness of datasets produced through most automated tracking techniques allows much more sub-structure in behaviour to be modelled. For example, whereas a relatively low-resolution time series may allow the estimation of transition rates on the scale of a day (i.e. estimating the probability of behavioural shifts from one day to the next throughout development), the highly resolved datasets typical of automated tracking

technology not only enable the estimation of those same day-to-day transition rates with greater accuracy, but also allow the estimation of transition rates between behaviours that occur on finer scales of hours or minutes [143–147].

Leveraging previously discussed approaches to define and classify behaviour (see §2*b*, ‘Data-driven definitions of behavioural axes’, and §2*c*, ‘Identifying behavioural classes and quantifying transitions among classes’), transition models (including Markov models) will allow us to address fundamental questions concerning the structure of behavioural development: when and to what extent are behavioural patterns during development path-dependent? Are behaviours operating at different timescales structured hierarchically (i.e. do distinct behavioural patterns consist of non-overlapping behavioural subclasses operating at shorter timescales)? Are individuals consistent not only in constituent behaviours but also in the transition rates among behaviours? Applied specifically to the study of individual behavioural variation across development, differences in individual-level behavioural plasticity can be quantified as changes to the structure of behavioural repertoires (i.e. behavioural transition matrices). Many state-switching models can also investigate how environmental cues influence behaviour by combining both behavioural and non-behavioural data as input [148] (see §2*a*, ‘Measurement innovations’). In total, these tools bring us closer to understanding the development of entire behavioural repertoires, the ‘architecture’ of behaviour throughout development and the factors that influence individual variation in developmental trajectories.

### (c) Information integration across development

Key to understanding behavioural development is understanding the cues to which developing organisms respond, how these cues are integrated with previous information available to animals, and how specific sequences of cues shape behavioural change [111,149–152]. In particular, Bayesian updating models have been very successful at describing behavioural development [111]. Briefly, Bayesian updating as it applies to developing animals is an information theoretic method for modelling an animal’s informational state (and consequently, optimal behavioural responses), given its prior information (based, for example, on evolutionary history or epigenetically inherited information [153,154]) combined with incoming, often imperfect, information through its current experience (or a sequence of experiences) [155]. While there are some empirical findings that corroborate predictions from Bayesian models of behavioural development [156–158], in general, empirical tests of these predictions remain relatively rare [111]. We believe that new experimental possibilities associated with high-resolution behavioural tracking—allowing us to track the unfolding of behaviour under different cue regimes over prolonged periods of time—put us in the position to test many of the untested predictions of Bayesian models of development.

The key predictions in Bayesian models of development relate (i) the structure of environmental fluctuations and (ii) the availability and quality of information to the degree and duration of behavioural plasticity [111,159]. As long as the environment does not change and animals receive a steady stream of informative cues throughout development, the observed degree of behavioural plasticity at an individual level (and, in some cases, behavioural diversity

at a population level) is predicted to decrease with age [107,108,136,160]. If, however, reliable cues are rare, if these reliabilities change through time, or if the environment fluctuates through time, periods of plasticity throughout development may be extended [109,110,160,161]. Likewise, cues received late in life might not elicit strong behavioural responses because they may be perceived to be associated with rare events or there may not be sufficient time left in life to capitalize on any benefits conferred through altering one’s phenotype [162]. Experimenters could manipulate ‘priors’ (e.g. by manipulating parental experience, or sampling from evolutionarily divergent populations), the structure of environmental fluctuations, and/or the reliability of cues during development and then follow behavioural change over development. This sort of approach could produce large enough datasets to estimate the entire developmental time course of changes in behavioural plasticity at an individual level, offering direct tests of many of the core predictions stemming from Bayesian models of behavioural development.

## 4. Limitations and future challenges

Big behavioural data are powerful tools with great potential to test fundamental open questions in behavioural development in the context of ecology and evolution (box 1). The wealth of data that high-resolution tracking provides, however, is limited in its scope to advance our knowledge of behavioural development without the idea-rich scaffolding that theory and hypothesis generation provide [163,164]. Thus, throughout this review, we have paid particular attention (see §3, ‘Using big behavioural data to uncover the principles governing behavioural development’) to how big data tools can both test and advance current theory in this field. Nevertheless, limitations remain that researchers must confront.

First, linking high-resolution behavioural tracking to metrics requiring terminal sampling (e.g. gene expression changes in the brain or experience-dependent epigenetic changes across development) will require creative experimental design and/or the development of new technologies (e.g. multi-electrode arrays or wireless neurotelemetry [165]). Further challenges arise when considering the combination of high-resolution behavioural and environmental time series. In some cases, salient environmental changes that have dramatic effects on behavioural development may occur only rarely (e.g. once or twice over the course of an individual’s development), limiting the ability of researchers to estimate their effects. These types of scenarios would make studies that look for correlations among environmental metrics from passive sensors and high-resolution behavioural data difficult; on the other hand, they may offer great opportunities for experimentally manipulating candidate environmental variables/stressors (their timing or intensity, for example) while tracking behavioural development. Next, while methodological advances allowing the collection of temporally rich behavioural data across development vastly reduce the amount of work effort per datapoint, a fundamental limitation that will always remain is the relative lifespan (in particular, the duration of development) of research animals. For species with long developmental periods, there are inherent challenges to collecting near-continuous developmental data. This might be partially addressed, for example, by subsampling populations of longer-lived species



**Box 1.** Representative major open questions in behavioural development and their big data approaches.

#### Behaviour–state connections

*Approach:* Detect presence of dynamic feedbacks between behaviour and state (i.e. bidirectional state–behaviour linkages); quantify both the strength and direction of state–behaviour feedbacks through development.

**Q1** What are the relative rates of change in behaviour and state during development and what are the dynamic consequences when they are linked?

**Q2** How common are state–behaviour feedbacks?

**Q3** How is the strength and direction of feedbacks affected by certain ecological conditions/selective environments?

**Q4** Are feedbacks more important in shaping developmental trajectories in particular developmental stages?

#### Early-life effects and behavioural transitions

*Approach:* Measure behavioural–experiential trajectories continuously throughout life; quantify fine-grained transitions between behavioural classes throughout development.

**Q5** What are the behavioural–experiential mechanisms linking early-life experiences and long-term behavioural outcomes?

**Q6** When and to what extent are behavioural patterns throughout development path-dependent?

**Q7** To what extent are behaviours that operate at different timescales structured hierarchically?

**Q8** Do individuals differ in their behavioural transition rates? Is this an ecologically important axis of behavioural variation?

#### Information integration across development

*Approach:* Pair high-resolution behavioural tracking data with similarly resolved monitoring of environmental cues.

**Q9** How are developmental responses to recent cues moderated by the specific sequences of past cues?

**Q10** How does behavioural development relate to the structure of environmental fluctuations?

**Q11** How does the availability and quality of information affect behavioural development?

by age class and conducting behavioural observations over shorter periods of development (relative to that species) but for individuals spread across age classes in order to get a fuller picture of development in the aggregate (e.g. combine approaches 4 and 5 in table 1). These and similar sorts of trade-offs will exist in most experiments in which researchers desire to test the whole of behavioural development, but the ever-growing technological advances in this field are also likely to continue to rebalance these trade-offs in favour of ever-richer behavioural developmental datasets across species.

## 5. Concluding remarks

For the last three-quarters of a century, a steady stream of technological advancement has allowed the discovery of new behaviours as well as innovations in the quantification of previously observed behaviours (e.g. audio recording of echolocation in bats [166] and cetaceans [167], spectrographic analysis of birdsong [168], high-speed cameras revealing feeding innovations [169,170], automatic sensing and social network analysis uncovering novel social and collective behaviours [65], machine learning algorithms as behavioural classifiers [89]). In turn, these technological advances in quantifying behaviour have been productively applied to understanding both the proximate and evolutionary causes

and consequences of behaviour [171], helping to transform the field of animal behaviour from a largely descriptive science to an analytical and theoretical one [172]. Now, with the widening application of state-of-the-art tracking technologies, the time is ripe to continue in this tradition by applying these tools to major open questions in one of behavioural ecology's foundational research cores: the ontogeny of behaviour.

**Data accessibility.** This article has no additional data.

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