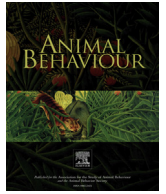




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Complex dynamics and the development of behavioural individuality

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CONSISTENTLY FINDING CONSISTENT DIFFERENCES

Animals in a population frequently display consistent among-individual differences in their behaviours (Bell, Hankison, & Laskowski, 2009; Wilson, 1998). Among-individual differences in behaviour have long been considered important as such differences are required for natural selection to cause mean individual behaviour to change. Indeed, in the last few decades increased interest in these differences has spurred the generation of the field of 'animal personality'. A key element of this recent surge has been to identify the processes that lead to and maintain among-individual behavioural differences. Correlations with more stable physiological or motivational states (Sih et al., 2015), or life-history traits (Réale et al., 2010), or the role of environmental factors (Kortet, Hedrick, & Vainikka, 2010; Montiglio & Royauté, 2014) have all been investigated to explain why animals in the same population show consistent differences in mean behaviour across contexts (Dingemanse & Wolf, 2010; Kight, David, & Dall, 2013). These explanations typically require there to be variation in some other factor, be that genetic or environmental in origin (e.g. Mathot, Dekinga, & Piersma, 2017), which then drives among-individual

differences in behaviour (but see: Luttbegg & Sih, 2010; Sih et al., 2015).

Recent empirical research, however, has found evidence for differences among individuals of the magnitude very commonly found in nature (Bell et al., 2009) in situations where substantial variation in other factors is lacking. Most recently, Bierbach, Laskowski, and Wolf (2017) found that among-individual differences in behaviour occur in Amazon mollies, *Poecilia formosa*, that did not differ in terms of genetic or environmental background. This was achieved by using clonal fish reared in identical tanks to reduce genetic and environmental variation. Similar results have been achieved in inbred eastern mosquitofish, *Gambusia holbrooki* (Polverino, Cigliano, Nakayama, & Mehner, 2016), and inbred house mice, *Mus musculus* (Brust, Schindler, & Lewejohann, 2015; Freund et al., 2013), although some degree of genetic variation is likely to persist in these latter examples. The authors suggested that finding consistent among-individual differences in behaviour in the absence of any measurable genetic and environmental variation is an unexpected result. This perception is based on an additive linear model of phenotypic variation, where phenotypic variation is the additive sum of genetic variation, environmental variation and gene-by-environment interactions. Under this paradigm, there is little room for consistent variation among individuals that is not related to variation in genotypes or the environment. Yet, this is exactly what the authors above found. So how did these animals come to show consistent behavioural differences?

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Bierbach et al. (2017) raised a number of potential explanations for the occurrence of individuality against common genetic and environmental backgrounds, including the intriguing possibility of maternal 'bet-hedging' through epigenetic variation (see also Groothuis & Trillmich, 2011), and positive feedback between state and behaviours (see also Sih et al., 2015). However, we would like to advocate an alternative explanation: that among-individual differences may arise out of very similar genetic and environmental backgrounds due to behavioural development being influenced by chaotic dynamics. Bierbach et al. (2017) concluded that individuality may be inherently unpredictable. That said, phenomena that are hard to predict but appear stochastic may often be driven by underlying deterministic forces (May, 1976). Weather systems are a good example of this, as they are driven by the deterministic dynamics of air movement, yet are difficult to predict accurately more than a few days or weeks in advance. Dynamics that are sensitive to initial conditions, and thus unpredictable, but unpinned by deterministic rules are often called chaotic dynamics.

CHAOTIC DYNAMICS

Reduced long-term predictability for systems with chaotic dynamics hinge on nonlinear relationships, where small initial differences in the parameters of the system can lead to much greater differences over time (Boyce, 1992; Hastings, Hom, Ellner, Turchin, & Godfray, 1993). Note that not all nonlinear systems are sensitive to initial conditions; some can show convergence to stable 'attractors' regardless of initial conditions (Northrop, 2011).

An example of a system driven by deterministic chaos that gives divergent results from small initial differences is a Lorenz attractor. A Lorenz attractor describes patterns of flow (fluid or air) around three 'saddle points' in three dimensions (Lorenz, 1963). Individual trajectories circle around one saddle point before flipping over to another, and so on (Fig. 1). Two points that are initially adjacent to one another will rapidly diverge along different trajectories. Therefore, any minute variation between two initial points will lead to potentially substantial differences between them at later time intervals, while any measurement error of initial conditions (which is virtually unavoidable in real-world systems) will render long-term predictions inaccurate.

The Lorenz attractor follows a series of differential equations, based on a continuous time model (for equations, see Fig. 1). The

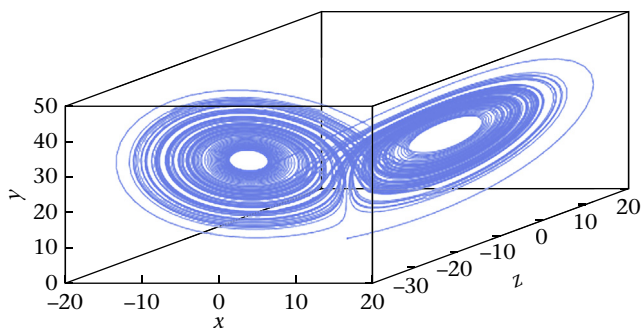


Figure 1. Near-identical initial conditions can lead to divergent locations over time. A Lorenz attractor, developed in the context of air and fluid dynamics, is a relatively simple mathematical model of how nonlinear relationships produce seemingly stochastic outcomes in atmospheric convection. The three-dimensional movement of the trajectories can be described using a set of differential equations, where $\dot{x} = \sigma(y - x)$, $\dot{y} = x(\rho - z) - y$ and $\dot{z} = xy - \beta z$. The parameters σ , ρ and β are constants that inform the nature of the trajectories. Figure reproduced in R v3.4.0 (R Development Core Team, 2016) with code from <<https://gist.github.com/RStyleNinja>> ($\rho = 26.48$, $\sigma = 10$, $\beta = 8/3$).

equations describe the movement of the trajectories in three dimensions (Fig. 1), which, when appropriately parameterized with certain constants (σ , ρ and β), produce oscillations and chaotic dynamics (Sparrow, 1982). The saddle points act as attractors so that the trajectories are kept within certain boundaries, rather than expanding into infinite space. While this may not necessarily be a suitable model to describe how consistent differences among individuals arise, since there are three axes that are continually varying, it is a good model for demonstrating how simple conditions and minimal initial variation can generate large amounts of variation over time.

The Lorenz attractor above describes changes in the state of the system in continuous time; similar chaotic dynamics can also be represented in discrete time models. An example of such discrete models is a simple dynamical growth model:

$$x_{t+1} = rx_t(1 - x_t) \quad (1)$$

where the value of x , bounded between 0 and 1, at time $t + 1$ depends on the value at the current time t , multiplied by the intrinsic rate of increase r (bound between 0 and 4), and how far the value is from the maximum (Verhulst, 1838, 1845). Following equation (1), r values below 1 result in extinctions (Fig. 2a), values between 1 and ≈ 3.57 give a single stable value (Fig. 2b) or oscillations among a set of values (Fig. 2c), regardless of the starting population size. Most values of r exceeding 3.57, however, give rise to chaotic dynamics, where no stable value is reached, and small initial differences in the starting values give very different results over time (Fig. 2d). There are however regions of r greater than 3.57 (around 3.84) where stable cycles can be achieved (Li & Yorke, 1975). The transitions between cycle regimes between 1 and ≈ 3.57 are related to the first Feigenbaum constant (≈ 4.6692 ; Feigenbaum, 1978). This constant is the limit of the ratio between the change in r required to double the number of values within a stable cycle (the number of values being the 'period'), and doubling of the number of values being a 'period doubling'. The ratio between the change in r required to go from one to two values, and the change in r to go from two to four values, and so on, converges on ≈ 4.6692 . This ratio in fact holds for all chaotic systems defined by an equation where one value is mapped to another, with a single quadratic maximum.

With respect to animal behaviour, one could consider x to be the level of the behaviour and t to represent the age of the organism being monitored. Small environmental, genetic, developmental or stochastic sources of initial differences would then lead to different trajectories for each individual (Fig. 2d). If these different trajectories were then translated into different mean levels of behaviour, and within-individual variation was not especially large, then we would detect significant among-individual variation. The trajectories are prevented from expanding into infinite parameter space by the negative frequency-dependent change inherent in equation (1). While neither the differential equations (Fig. 1) or the difference equations (equation (1), Fig. 2) may be directly mappable to individual behaviour development, they may be useful starting points for understanding how chaos can cause small initial differences to lead to greater differences over time.

If behaviour is chaotic, with trajectories moving unpredictably around in phenotype space, how would consistent among-individual differences be maintained? A simple answer is that behavioural variation may be chaotic during early development, but this chaotic period may end upon maturity, allowing individual trajectories to be maintained. This is perhaps similar to the way that young animals tend to imprint on or copy from conspecifics at an early age, but upon maturity this ceases (Bateson, 1966; Immelmann, 1975). Such sensitive periods may be adaptive (Panchanathan & Frankenhuis, 2016), and so chaotic periods may

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