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Title

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Permalink

<https://escholarship.org/uc/item/33m2x24p>

Journal

Trends in ecology & evolution, 30(1)

ISSN

0169-5347

Authors

Sih, Andrew
Mathot, Kimberley J
Moirón, María
et al.

Publication Date

2015

DOI

10.1016/j.tree.2014.11.004

Peer reviewed

Animal personality and state–behaviour feedbacks: a review and guide for empiricists

Andrew Sih¹, Kimberley J. Mathot^{2*}, María Moirón², Pierre-Olivier Montiglio¹, Max Wolf³, and Niels J. Dingemanse^{2,4}

¹ Department of Environmental Science and Policy, University of California, Davis, CA 95616, USA

² Evolutionary Ecology of Variation Research Group, Max Planck Institute for Ornithology, Seewiesen, Germany

³ Department of Biology and Ecology of Fishes, Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Berlin, Germany

⁴ Behavioural Ecology, Department of Biology, Ludwig Maximilians University of Munich, Planegg-Martinsried, Germany

An exciting area in behavioural ecology focuses on understanding why animals exhibit consistent among-individual differences in behaviour (animal personalities). Animal personality has been proposed to emerge as an adaptation to individual differences in state variables, leading to the question of why individuals differ consistently in state. Recent theory emphasizes the role that positive feedbacks between state and behaviour can play in producing consistent among-individual covariance between state and behaviour, hence state-dependent personality. We review the role of feedbacks in recent models of adaptive personalities, and provide guidelines for empirical testing of model assumptions and predictions. We discuss the importance of the mediating effects of ecology on these feedbacks, and provide a roadmap for including state–behaviour feedbacks in behavioural ecology research.

State–behaviour feedbacks and the emergence of personality differences

The past decade has seen tremendous interest in animal personalities [1–3], stemming from accumulating evidence for individual repeatability and significant correlations between various behaviours (e.g., boldness, aggressiveness, activity, exploration, or sociability). Empirical studies show that animal personalities and behavioural syndromes (correlations across contexts) vary as a function of ecology [4,5]; for example, aggressiveness and boldness are often positively correlated but the strength of this correlation varies depending on the predation regime [6,7]. Variation in syndrome structure also exists across different temporal scales; for instance, early experiences (e.g., exposure to stressors) can have large effects on the development of personality structure but such effects can

either be temporary or permanent [8–10]. Understanding the processes explaining the emergence of personality differences and variability of syndrome structure within and among species represents a major current topic in adaptive personality research.

Although personality has been examined in numerous species, most studies are descriptive in nature, documenting patterns of behavioural structure. Over the past few years, however, theory has been developed to explain the existence of animal personalities from an adaptive perspective. Most of this theory invokes adaptive state-dependent behaviour, explaining personality as an adaptive outcome of among-individual differences in state [11–13]. Building on earlier work by Rands *et al.* [14] and Dall *et al.* [15], recent models have focused on the joint emergence and maintenance of among-individual differences in behaviour and state, and how such differences are promoted by positive feedbacks between behaviour and state. These models (both mathematical and verbal) have generated testable predictions for a broad range of scenarios. The time is now ripe for more tests of the predictions of those models. Here, we present a framework that unifies the logic of numerous recent models in a fresh way and paves the way for rigorous testing of these models. Specifically, we: (i) describe the core idea underlying all feedback loops thereby uniting numerous mechanisms and models; (ii) discuss how this core idea can integrate the study of proximate and ultimate mechanisms, potentially over ecological, developmental, and evolutionary time scales; (iii) summarize predictions of these models on variation in animal personalities; and (iv) offer guidance to empiricists for studying state–behaviour feedbacks, and for testing predictions on how these feedbacks relate to personalities.

Feedback loops and variation in personalities – the core concept

Although behaviour in principle can be infinitely flexible, behavioural repeatability can potentially be explained by among-individual differences in slower-changing or even fixed state variables, in combination with adaptive state-dependent behaviour ([11,12,15,16]; Table 1). Individuals thus differ in behaviour because they differ in state and

Corresponding author: Sih, A. (asih@ucdavis.edu).

Keywords: adaptive theory; aggression; animal personality; asset protection; boldness; exploratory tendency; feedback loops; phenotypic integration; social niches; state-dependent behaviour.

*Current address: Marine Ecology Department, Royal Netherlands Institute for Sea Research, P.O. Box 59, 1790 AB Den Burg, The Netherlands.

0169-5347/

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Table 1. Overview of mechanisms and models generating dynamic feedbacks between state and behaviour

Mechanism	State ↔ behaviour	Predicted feedback	Assumptions	Key factors	Type ^d	Refs
<i>(i) Feedbacks involving intrinsic state variables</i>						
Asset protection	RRV ^a ↔ willingness to take risks ^b	Positive feedback: emerge in scenarios where more risky actions decrease assets compared to less risky actions. Negative feedback: emerge when more risky actions increase assets.	Risky actions increase or decrease assets compared to less risky actions; these effects can work via fecundity or mortality.	Effect of risky actions on fecundity and mortality schedule	M	[16,18,20,61]
Starvation avoidance	Energy reserves ↔ sampling ^c	Positive feedback: under low starvation risk, only individuals with high energy reserves can 'afford' to sample, which allows them to track resources and maintain higher long-term intake rates than non-samplers. Negative feedback: under high starvation risk, individuals with low reserves sample for survival. Sampling allows them to build energy reserves, eroding among-individual differences in energy reserves and sampling.	Sampling behaviour involves immediate costs (e.g., sampling errors), but allows higher long-term intake rate through tracking of resources.	Probability of energetic shortfall	M	[26]
Starvation avoidance	Energy reserves ↔ boldness while foraging	Positive feedback: individual with lower energy reserves is more willing to take risks, but never increases in state relative to individuals with high reserves because individuals with high reserves always forage as part of a pair, allowing them to forage more efficiently. Negative feedback: poor condition individuals are forced to be bold because of the need to forage, and foraging builds energy reserves. High condition individuals are less bold and therefore they do not increase reserves as quickly.	Foraging in pairs is advantageous because it lowers predation risk and/or increases energetic gain.	Social environment (i.e., solitary versus group foraging)	M	[14,16,62]
State-dependent safety	Size, energy reserves, condition, vigour ↔ boldness in foraging context	Positive feedback: individuals in good condition behave more boldly, thereby increasing in condition.	Individuals with higher state face lower risk of predation while being bold.		M	[16]
State-dependent immune function	Host immune function ↔ boldness, activity	Positive feedback: high resource intake leads to efficient immune function, and individuals with efficient immune function are better able to cope with the potential exposure to parasites that results from high foraging effort (e.g., boldness and activity).	High resource intake rates lead to efficient immune function.		V	[22]
State-dependent foraging strategy	Gape size ↔ cannibalistic behaviour	Positive feedback: individuals with larger gape-size are more cannibalistic, thereby increasing in size and reinforcing their tendency to be cannibalistic. Negative feedback: predation risk reduces cannibalism since predators preferentially attack cannibalistic individuals, which become less active, and thus, less likely to encounter potential cannibalism victims. Consequently, there is no reinforcement of cannibalism or size differences.	Cannibalism increases growth rate due to an increase in foraging efficiency. Predation risk reduces cannibalism either through non-consumptive or consumptive effects.	Predation risk	E	[24]
Learning or skill improvement	Experience with responsiveness ↔ responsiveness	Positive feedback: initial differences in responsiveness are maintained.	Individuals that have been responsive in the past face lower costs (or higher benefits) of being responsive again.		M	[28]
Winner/loser effects	Winning or losing experience ↔ aggressiveness	Positive feedback: individuals that have recently experienced a 'win' in an agonistic encounter are more likely to initiate future agonistic encounters. Individuals initiating agonistic	Initiating an aggressive encounter increases the likelihood of winning.		V	[63]

Table 1 (Continued)

Mechanism	State ↔ behaviour	Predicted feedback	Assumptions	Key factors	Type ^d	Refs
		encounters have a higher probability of winning, reinforcing individual differences in winning experiences and aggressiveness. The strength of the loop would probably differ between winners and losers since winner effects are distinct from loser effects, and often have memory times.				
Hormone-mediated perception of hunger	Insulin levels ↔ feeding behaviour	Positive feedback: high levels of insulin lead to overeating due to increased perception of hunger, and weight gain increases insulin levels.	High insulin levels trigger overeating behaviour.		E	[64]
State-dependent energy assimilation efficiency	BMR ↔ behaviours that increase resource acquisition	Positive feedback: large metabolic machinery (e.g., stomach, intestines) is necessary to process high volumes of energy. Acquiring and processing high volumes of energy facilitates the maintenance of energetically costly organs that are needed for energy processing.	High energy processing ability promotes expression of behaviours that increase energy acquisition rate.		V	[13,65–67]
<i>(ii) Feedbacks involving extrinsic state-variables</i>						
Aggressiveness mediated by other individuals' aggressiveness	Aggressiveness individual 1 ↔ aggressiveness individual 2	Positive feedback: individuals that are more aggressive are more likely to elicit aggressiveness in others.	Simultaneous effect in interacting phenotypes.		V	[68]
Parasite-mediated changes in energy expenditure	Parasite infection ↔ boldness activity	Positive feedback: parasite infection increases energetic needs, favouring high levels of boldness activity to secure resources. Animals that are more bold-active are more likely to encounter and become infected by parasites.	Parasite infection imposes non-negligible energetic costs.		V	[49]
Anthropogenic contaminants (ACs)	Exposure to AC ↔ risky behaviours	Positive feedback: animals that are exposed to ACs decrease survival or increase reproductive effort, favouring an increased expression of risky behaviour. This further exposes them to ACs, reinforcing differences in survival or reproductive effort. Negative feedback: toxic effects of exposure to ACs lead to overall decrease in risky behaviours, reducing future exposure to ACs.	Exposure to ACs changes optimal allocation of energy to growth, reproduction and maintenance and/or has toxic effects that impair the function of the organism.	Toxicity	V	[54]
<i>(iii) Joint evolution of behaviour and state variables</i>						
Co-evolutionary diversification	Model applies to a diverse range of behaviours and state variables	Positive feedback: promotes the evolutionary emergence of correlated differences in state and behaviour.	State variable affects the cost and/or benefits of behaviour; behavioural trait is under negative frequency-dependent selection.	Increases in the evolving state variable are costly to individuals	M	[55]

^aRRV, residual reproductive value, i.e., future fitness expectations.

^bAny behaviour that increases access to resources at the cost of an increased risk of mortality.

^cInvestment of time and/or energy to reduce uncertainty about alternative foraging options.

^dType of paper from which predictions were derived: E, empirical; M, model; V, verbal argument.

adjust their behaviour in an adaptive fashion to these differences. In behavioural ecology, the state of an individual includes any features that affect the cost and benefits of its behavioural actions [17]. Often, these involve labile characteristics of the focal individual such as its energy reserves, condition or vigour, reproductive value, physiology (metabolic rates, hormone levels, or immune state), morphology, or colour, age, or size. They could also include the individual's information state, skill set, social rank, or role.

Importantly, state variables are not restricted to features of the focal individual but include also characteristics of its social environment (e.g., its local density or sex ratio, or the behaviour or other traits of its social partners), or aspects of its ecological environment (e.g., its predators, competitors, or parasites). Consistent differences among individuals in any of these features can, in combination with adaptive state-dependent behaviour, explain consistent differences among individuals in behaviour.

When state variables are themselves labile, the question shifts to: what explains consistent individual differences in both the labile state variables and behaviour? Recent models emphasize that positive feedbacks between state variables and behaviour can link the co-evolution or co-development of state and behaviour that can then drive divergence and persistence of long-term differences in both (Figure 1, Box 1, Table 1), thus resulting in consistent among-individual variation in behaviour (cf. personality) and state. By contrast, negative feedbacks result in convergence in state and behaviour, and thus no long-term persistence of differences in either. Note that with feedbacks, the state variable no longer needs to be inherently stable or slow-changing – feedbacks between two potentially rapidly changing variables can stabilize both. Whether feedbacks are positive or negative depends on the selective landscape. Positive versus negative feedbacks should evolve by means of positive versus negative correlational selection for optimal combinations of state and behaviour. Positive feedbacks, in particular, are favoured if a behavioural tendency produces a change in a state variable that increases the net benefit of maintaining or even increasing that behavioural tendency (cf. adaptive phenotypic plasticity; Box 1). In the following section, we summarize models and ideas on state variables, feedback dynamics, and predictions about variation in personality (Box 1, Table 1).

Feedback loops: an overview of models and mechanisms

Various models of feedbacks between state and behaviour have been proposed (Table 1). In the following sections we

discuss three main types: (i) state–behaviour feedbacks involving intrinsic state variables; (ii) state–behaviour feedbacks involving extrinsic state variables; (iii) co-evolutionary feedbacks.

(i) State–behaviour feedbacks involving intrinsic state variables

We use intrinsic state variables to mean state variables that are features of the same individual that is expressing the behaviour; for example, an individual's level of fat reserves, hormones, metabolic rate, residual reproductive value (RRV, see below), etc.

Feedback loops involving risk–reward and life history trade-offs. Perhaps the most widely recognized mechanism explaining personality differences connects variation in life history strategies to personalities where the key state variable is the individual's RRV, roughly speaking, it's expected future reproductive success (or 'assets') [18]. According to the asset protection principle [19], the higher the assets of an individual, the less willing that individual should be to risk its life for a given benefit, as the assets of an individual determine what it stands to lose in the case of death. Differences in assets are thus predicted to give rise to differences in all kind of risk-related behaviours like boldness and aggressiveness, with higher-asset individuals being more cautious. Positive feedbacks occur if: (a) being cautious means reducing current reproductive effort and investing instead in future reproduction (thus increasing RRV), and conversely, (b) if the risky behaviour of low-asset individuals tends to increase current reproductive success, but at the cost of decreases in future RRV

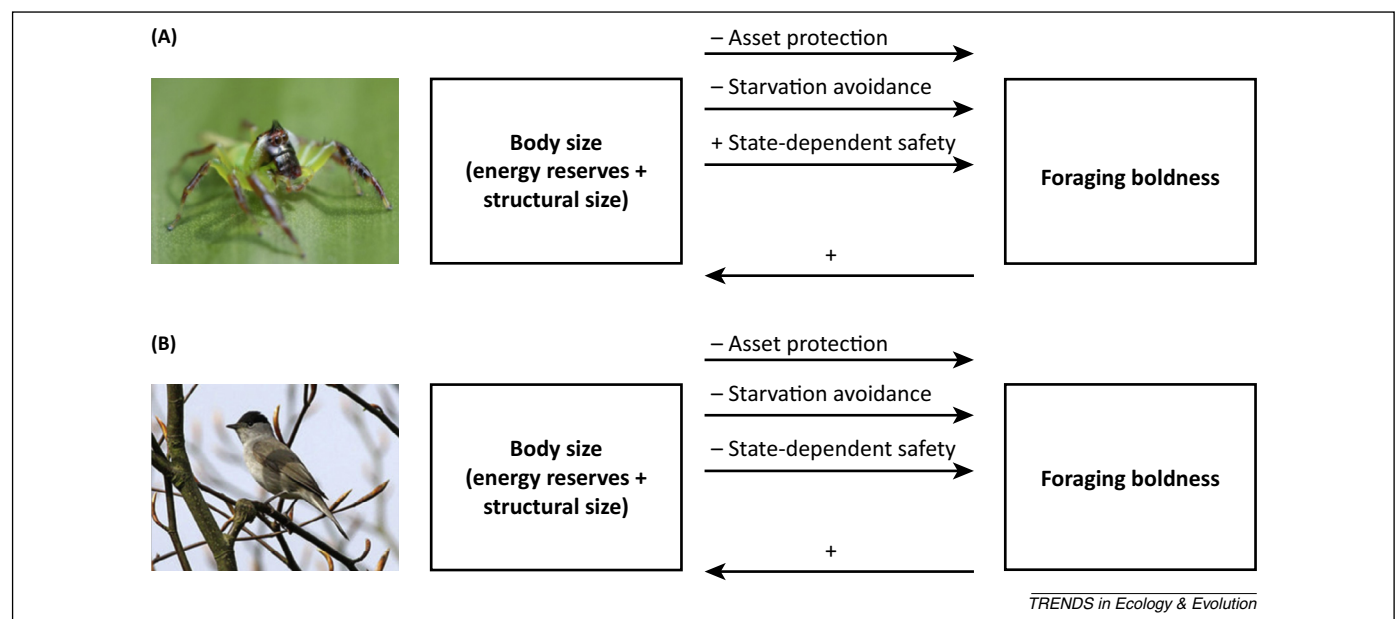


Figure 1. Illustration of how multiple mechanisms can simultaneously shape feedbacks between state and behaviour. Foraging boldness allows individuals to accrue more resources and increase their body size (either through growth or accumulation of energy reserves). However, the effect of body size on behaviour differs depending on the mechanism underlying the relationship. Asset protection predicts a negative feedback that drives large individuals to avoid risky behaviours, and starvation avoidance predicts negative feedback that drives small individuals to take risks while foraging. Additionally, depending on the species, larger body size/energy reserves can provide safety benefits (e.g., larger jumping spiders, *Phidippus princeps*, are better at escaping predators [69]; panel A) or reduce their escape performance (e.g., larger blackcaps, *Sylvia atricapilla*, have reduced predator evasion [70]; panel B). When the different mechanisms produce loops with differing directions (A), the net direction of the feedback between state (e.g., body size) and behaviour (foraging boldness) will depend on the relative importance of each of these mechanisms, which varies as a function of predation risk and resource level (i.e., the feedback outcome can be explained as match/mismatch between risk and rewards [16]). Photos obtained via Wikimedia commons.

Box 1. Feedbacks: integration of proximate and ultimate approaches

Animal behaviourists commonly distinguish between proximate versus ultimate approaches for explaining observed behaviour (but see [71]). The usual idea is that proximate explanations invoke underlying mechanisms; for example, how physiology, hormones, neurosensory, or cognitive mechanisms might explain observed behaviours. By contrast, adaptive, ultimate approaches attempt to explain behavioural patterns using cost–benefit considerations; animals exhibit behaviours that enhance fitness. The state–behaviour models described here integrate these two by solving for the best behaviour given the organism's state (the proximate mechanism). That is, these models explicitly unify adaptive (ultimate) and mechanistic (proximate) views. To choose which model to use to explain observed behaviours in a given system, the behaviourist must match their system to the relevant state variable (see Guide for empiricists). One important point is that because the models emphasize feedback loops, the emphasis is on the joint unfolding of the back-and-forth feedback between the organism's behaviour and its physiology (or other state variables) on short-term, developmental, or evolutionary time scales (i.e., state is a proximate underpinning of behaviour, and vice versa). Because many of the models track changes in behaviour and a state variable (e.g., condition, energy reserves, or RRV) over long periods of time, the models make predictions on the development of behaviour (and state variables) over ontogeny [8]. With positive feedbacks, early experiences (that affect early differences in state) have large effects on later 'personality type', whereas with negative feedbacks even large differences in early state are predicted to have little effect on later personality. Thus the state–behaviour feedback framework suggests that developmental sensitive time windows (where experiences during the window govern later phenotypes) are not an invariant feature of a developmental system, but are instead an adaptive outcome of positive feedback loops. Finally, note that this framework substantially expands the usual view of what is a 'proximate mechanism'. Instead of focusing primarily on physiology or neuroendocrine mechanisms (and perhaps associated genetic mechanisms), the relevant state variables could be any factor that influences adaptive behaviour and, in turn, is influenced by the behaviour. As noted in the text this can include a broad range of individual traits, as well as traits of other individuals (e.g., social partners), or even of other species (e.g., parasites).

(e.g., via exposure to parasites) [20]. In essence, positive feedbacks favour either a fast lifestyle associated with bold, aggressive, risky behaviour and rapid reproduction, or a slow lifestyle with cautious behaviour and delayed reproduction [21]. Asset protection, however, can also produce negative feedbacks if, for example, being bold results in increased assets (e.g., increased energy reserves) while being cautious results in an erosion of assets. This negative feedback would tend to produce convergence in assets and behaviour, and thus no long-term persistence of differences in personality.

While the above arguments are based on the prediction that high-asset individuals are more cautious, higher assets in the form of higher condition can also favour higher risk-taking [16]. For example, prey often enjoy state-dependent safety where larger, stronger, more vigorous prey are better at escaping from or defending against predators, and thus suffer lower costs of predation risk while foraging than weaker prey (see [16] for references). The lower cost allows high condition animals to forage actively and thus continue to bring in the energy to maintain their high condition. By contrast, animals in poor condition should not take risks if they can be easily

captured. Because they hide instead, they take in little energy and stay in poor condition (i.e., animals in poor condition make the best of a bad job). Similar logic can generate positive feedback loops involving state-dependent resistance against parasites [22]. Hosts in better condition might have more effective immune systems that allow them to be bold and active (and thus gain the energy to stay in good condition) even if this exposes them to more parasites.

Condition-dependent foraging success can also generate positive feedback loops [23]. Game theory predicts that if the costs of fights are high then only animals in good condition (with high resource holding potential, RHP) should be aggressive, while those in poor condition should be unaggressive since they have a low chance of winning. High RHP, aggressive individuals then gain resources that keep them in superior condition, while low RHP, unaggressive individuals settle for less and remain in poor condition and thus unaggressive. An extreme case of this phenomenon involves condition-dependent cannibalism as the mechanism that generates the positive feedback that maintains individual differences in condition and behaviour [24].

Finally, risk in the sense of uncertainty (e.g., about the best foraging options, breeding sites, etc.) can generate feedbacks between energy reserves and behaviour. Individuals that sample and learn about alternative foraging options can potentially gain more energy in the long-term but suffer short-term costs due to sampling (i.e., checking the state of an option that is currently unprofitable [25,26]). Under high immediate risk of starvation, individuals in the poorest energetic state are expected to sample because the only means of achieving sufficient energy intake is to locate the most profitable feeding options, that is, 'sampling for survival' [26]. Because sampling will allow individuals with low energy reserves to build reserves, the feedback between sampling behaviour and energy reserves is negative, and individual differences in energy reserves and sampling behaviour will tend to erode over time. The situation reverses to a positive feedback loop when there is a low immediate risk of starvation. Then, individuals with lower energy reserves should not sample, because sampling errors will significantly increase their probability of starvation. Instead, only individuals with high energy reserves are expected to be able to afford the 'luxury' of sampling, because for them, the short-term costs of sampling are not enough to increase their probability of starvation [26].

Feedbacks involving an individual's skill set or experience. An individual's skill set is another key state variable. Often, the more experience an individual has with a particular behaviour, the better the individual gets at performing that behaviour which makes it advantageous for the individual to stick to that behaviour [11,27]. This positive feedback between behaviour and the experience that an individual has with this behaviour thus favours consistency. Moreover, when selection on different behavioural alternatives is negatively frequency-dependent, this feedback is predicted to promote consistent, among-individual differences in behaviour [28];

note that frequency-dependent selection alone does not predict consistency [29].

The behaviour–experience feedback can also work for more complex behavioural phenotypes associated with differences in social roles, social niches, or positions in a social network [30,31]; that is, personality differences can be understood as social niche specializations [30,32]. Here, the state variable is the individual's social role, niche, or position. More broadly, the key state variable can be any ecological or social situation that is experienced by focal individuals (see below, feedbacks involving extrinsic state variables). Positive feedbacks can emerge if different social roles–niches–positions drive differences in behaviour that in turn reinforce the individual's social role–niche–position. For example, subordinate individuals might forage in low-quality patches to avoid competing with dominants over food, however, this patch choice can then prevent them from gaining the resources required to gain dominance, thereby reinforcing their subordinate position. This is a special case of the general idea that situation choice facilitates the evolution of specialization [33].

Hormone–behaviour feedbacks. Individual differences in hormone levels can drive differences in behaviour. Behaviour, in turn, can affect hormone levels. For example, high testosterone can increase aggressiveness, but aggressive behaviour can also drive up testosterone levels, giving rise to a positive feedback. Positive feedbacks also exist between social behaviours and oxytocin [34–36], and between behaviour, life histories, and corticosterone responses [37,38]. Of course, neuroendocrine systems themselves are characterized by feedbacks [39,40] and these feedbacks can potentially stabilize personalities even if behaviour does not strongly affect hormones [37].

Hormones can also serve as an important mediator of feedbacks between other intrinsic or extrinsic state variables and behaviour. For example, behaviour–parasite feedbacks (discussed below) are often mediated by effects of parasites on host hormone levels [41,42] and, in some cases, appear to involve adaptive parasite manipulation of host neuroendocrine pathways [43,44]. Progress in understanding feedbacks between behaviour and multiple, interacting components of the overall neuroendocrine system should be invaluable for better understanding personalities.

(ii) State–behaviour feedbacks involving extrinsic state variables

Other models emphasize that state variables that shape an individual's personality need not be a trait of the focal individual, but can instead be a characteristic of a conspecific, members of another species (e.g., parasites), or some other external factor such as an environmental contaminant.

An example involves the feedback between the predictable part of a focal individual's behaviour (cf. its 'personality') and the responsiveness of its social partners. If the focal individual's behaviour is consistent (and thus predictable), this favours social partners that are paying attention

(responsive). Conversely, if social partners are responsive, this can favour the focal individual being predictable. Being predictable can be favoured if it allows an individual to build a reputation (e.g., for being aggressive or cooperative) that manipulates a socially responsive partner's behaviour in a mutually beneficial way (e.g., to back off without a fight, or to cooperate [29,45]). Similarly, the behaviour–predictability feedback is predicted to promote consistency (via a form of correlational selection that favours individuals continuing to do what they have done in the past) in leader–follower situations [45,46] and in contexts of social niche specialization [30]. Other feedback loops involving the reciprocal behaviours of two or more individuals include effects of the aggressiveness of individual X on individual Y and vice versa [47], and personality-dependent, predator–prey behavioural response games [48].

A fascinating example of where the state variable is another species involves parasites. Individual differences in encounters with parasites due to small differences in behavioural tendencies or just to chance can affect the individual's subsequent behaviour [22,49,50] in ways that generate long-term, consistent, among-individual differences. If carrying a parasite load increases host energy demands without reducing host vitality, the result can be an increase in activity or exploratory behaviour (to 'feed' the parasite) that further increases parasite loads (i.e., positive feedback). Parasites can also manipulate host behaviour to enhance parasite transmission to the next host [51]. For example, parasites can make their hosts more active or bold, thus picking up more parasites until the host's highly conspicuous behaviour causes them to be noticed and eaten by the parasite's next host [52]. As this process unfolds, the positive feedback loop can help explain the persistence of consistent personalities. Conversely, a negative feedback loop can exist if parasites weaken their hosts (and thus reduce host activity) or reduce their host's tendency to be sociable (thereby reducing encounters with other infected hosts).

Finally, state–behaviour feedbacks involving non-living, extrinsic factors can also generate personality. For example, if environmental chemicals influence behaviour in ways that increase the likelihood of being further exposed to chemicals, then even chance variation in initial encounters with contaminants, such as pesticides, heavy metals, or pharmaceuticals, could generate lasting among-individual differences in behaviour [53,54].

(iii) The joint evolution of behaviour and state variables

Most of the models discussed above assume that animals adjust their behaviour to their state in an adaptive way (e.g., animals with higher assets increase their fitness by being more cautious). Most also assume, however, that the converse need not hold; that is, while behaviour affects the state variable (e.g., bolder foraging increases energy reserves), the state variable is not adjusting adaptively to the behaviour. An alternative view explicitly models how behavioural consistency can emerge from the co-evolution or co-development of an adaptive, integrated phenotype where both the behaviour and state respond

adaptively to the other. For example, in the classic hawk–dove game, in the absence of a co-evolving state variable, selection favours individuals that exhibit behavioural inconsistency (i.e., individuals that switch between hawk and dove behaviours in repeated interactions). If, however, behaviour co-evolves with physiological state variables (e.g., metabolic capacity), the result is the evolution of alternative, consistent personalities with associated differences in physiology: low-metabolism individuals that are unaggressive versus high-metabolism individuals that are aggressive [55]. High metabolic capacity helps animals win fights that bring in the energy to offset the costs of maintaining a high metabolic capacity. Extending the scenario to allow for a second behavioural trait (boldness) that is also affected by the physiological state variable, this model predicts the co-evolution of positive correlations between metabolic rate, aggressiveness, and boldness. Although this model is couched in terms of co-evolving physiological state variables, the underlying concepts apply to any co-evolving morphological, cognitive, or life history trait that affects the costs or benefits of behavioural actions [55]. Thus this model formalizes the basic logic underlying the Pace of Life syndrome [21] or life history-productivity syndrome [13] ideas that posit the co-evolution of fast versus slow general lifestyles including physiology, behaviour and life histories, and of fast/slow cognition syndromes [56].

Multiple simultaneous feedback loops

Several of the above examples illustrate how a single mechanism (e.g., asset protection or starvation avoidance) can generate either positive or negative feedbacks depending on other factors. In other cases, state-dependent behaviour can be simultaneously shaped by mechanisms with contrasting feedback patterns (Figure 1). When the feedbacks do not all operate in the same direction, the net direction of the feedback loop will depend on the relative contribution of each mechanism, which is likely to vary as a function of ecological conditions (e.g., predation risk, food availability, etc.) [16].

Guide for empiricists

We next provide a guide for studying state–behaviour feedback loops and for testing predictions on how those loops influence animal personalities (Boxes 2 and 3). While one could start with a model and search for a system that appears to fit that model, we assume, for this guide, that the empiricist is already studying a particular system and seeks to identify and test models that can potentially explain variation in the structure of personality in that system.

Because the various models revolve around different state variables, it is important to identify which state variables are good candidates for a state–behaviour feedback loop in one's system. Although feedback loops are dynamic processes that play out over time within an

Box 2. A worked example

To illustrate our guide to empirically testing state–behaviour feedback loops, we provide an example with cannibalism as the focal behaviour and gape size in salamander larvae as the state variable.

(i) Identify the system and the mechanism. The first step is to identify a system and a mechanism that fits the system. In this case, we focus on a state-dependent foraging strategy model as the mechanism and larval salamanders as the species. Many salamander larvae exhibit size-dependent cannibalism, especially under high population densities. These interactions induce an increase in gape size within populations that allows conspecific predation, and also an increase in foraging efficiency since conspecifics represent a rich resource. However, under high predation risk, salamander larvae reduce their foraging activity in order to avoid risky encounters. The relative importance of each mechanism will influence the net direction of the feedback loop.

(ii) Predictions. See the predictions for positive and negative feedbacks of this model ('State-dependent foraging strategy') in Table 1 in main text.

(iii) Experimental approach. The most straightforward experimental test is to manipulate the body size of salamander larvae (e.g., by experimentally increasing food availability) as a proxy for gape size to investigate whether this manipulation results in the predicted effect on cannibalistic behaviour, and vice versa. In some cases, experimental manipulations of state and/or behaviour may not be feasible or even necessary. Non-experimental studies can also be suitable tests of state–behaviour feedback loops since natural variation in both variables can provide enough initial differences among individuals to initiate the dynamics. For instance, Kishida *et al.* [24] empirically studied this mechanism and system based on baseline initial variation among individuals.

A complementary experimental test is to manipulate the ecological conditions to test for predicted changes in the feedback loop direction. Theoretical models allow us to predict the feedback outcome based on match/mismatch between risk and rewards [16]. For instance, feedbacks between gape size and cannibalism can vary as a function of

predation risk and resource level. One experiment can keep resource levels constant (here, salamander larvae density) and manipulate predation risk by adding larval dragonflies (top predators of amphibian larvae). The ecological prediction is that positive feedbacks should predominate in conditions of intermediate ecological favourability while negative feedbacks should predominate in highly favourable or highly unfavourable conditions [16].

In both cases, manipulative or not, repeated measurements of behaviour and state of the same individual and for different individuals are essential. Salamander larvae present continuous growth until metamorphosis, and therefore, changes in size (and gape size) can be measured daily over the entire larval period. In terms of behaviour, cannibalistic tendency can also be assessed regularly over the same period. The required data (i.e., number of measurements) will depend on the effect size of each variable, and consequently, on the statistical power.

(iv) Statistical analysis. To analyse the relationship between number of salamanders cannibalized and gape size, we can use a 'reaction norm' approach [58,72] where time is fitted as the environmental (*x*) axis [73] to estimate how cannibalistic behaviour and gape size change within individuals over time. We would, as a first step, statistically fit a random regression mixed-effect model that would enable us to estimate the statistical parameter (cf. intercept/slope correlation) that informs us on whether state and behaviour indeed showed patterns of 'fanning-out' (cf. among-individual divergence) or 'fanning-in' (cf. among-individual convergence) as expected when there were feedback loops in action (see Figure 2 in main text). As a second step, we would fit a bivariate random regression model, where cannibalistic behaviour and gape size were both fitted as the two response variables, and quantify the covariance between the slopes of the two temporal reaction norms (for guidelines, see [60]). In the presence of feedbacks (whether positive or negative), the slopes of the reaction norms for behaviour and gape size would be correlated. See the text, Box 3, and Figure 2 in main text for more details.

Box 3. Feedbacks in equations and statistical analyses of phenotypes

Feedbacks between phenotypic traits are often described mathematically using multivariate phenotypic equations with simultaneous relationships [74,75]. A simple example is represented by the following 'double' equation (Equation 1):

$$y_{t,s} = y_{t-1,s} + \lambda_{b \rightarrow s} y_{t-1,b} + e_{t,s} \quad [1a]$$

$$y_{t,b} = \lambda_{s \rightarrow b} y_{t,s} + e_{t,b} \quad [1b]$$

Where $y_{t,s}$ and $y_{t,b}$ represent state and behaviour, respectively, of a single individual at time t . Here, the first part of the equation (Equation 1a) captures the notion that an individual's current state is equal to its previous state ($y_{t-1,s}$) apart from a modification due to its previous behavioural action ($y_{t-1,b}$), where the dependence of current state on previous behaviour is given by $\lambda_{b \rightarrow s}$. The second part of the equation (Equation 1b) captures the notion that an individual's current behaviour is a function of its current state ($y_{t,s}$), where the dependence of current state on previous behaviour is given by $\lambda_{s \rightarrow b}$. Both models have residuals ($e_{t,s}$, $e_{t,b}$) and would in reality also incorporate a multitude of fixed effects (e.g., age) that are ignored here for simplicity.

The magnitude and sign of the feedback loop (L) between state and behaviour can be quantified by multiplying the effect of current state

on current behaviour ($\lambda_{s \rightarrow b}$) with the effect of current behaviour on future state ($\lambda_{b \rightarrow s}$). An important characteristic of Equation 1 is that positive feedback will result in an infinite increase in individual differentiation over time (see Figure 2A,D in main text). In reality, we would expect biological floors and ceilings to both state and behaviour, resulting in the stabilisation of individual differentiation with time. Statistically, this can be implemented by specifying non-linear effects of state on behaviour (and vice versa).

The simultaneous relationships between state and behaviour exemplified in our worked example can be quantified statistically using structural equation modelling for datasets where state and behaviour have both been assayed repeatedly on the same individual [74,75]. The approach can also be extended to quantify individual differences in feedback loops when implemented in a mixed-effect modelling framework [57]; such variation is expected because ecological conditions should shape the magnitude and sign of feedbacks in nature [16]. Finally, cases where a focal individual's behaviour represents the state of another individual (cf. interacting phenotypes) can be captured by fitting a single phenotypic equation with two random effects (individual and social partner identity), where the feedback loop can be calculated directly from the covariance between the two random effects [68].

individual, they should often also generate among-individual state–behaviour correlations. For example, if hosts that are more active pick up more parasites that then make those hosts even more active, we expect development of an among-individual, positive (host activity vs. parasite load) correlation. A first step can thus be to screen for among-individual state–behaviour correlations. When some data are available on temporal consistency, focus on state variables that have a similar level of temporal consistency as behaviour. For example, behaviours that exhibit life-long stable differences among individuals are more likely to be connected to stable state variables (e.g., morphology, life history type, or a stable social role) than with day-to-day variation in the social environment. Identifying good candidate state variables leads the empiricist to one or a few of the models in Table 1. Next, check to make sure that your system fits key assumptions of those models.

Having identified relevant state variables, if possible, manipulate these experimentally (e.g., alter energy reserves or parasite loads) to assess effects on behaviour. Following behaviour over longer periods of time will provide insights into feedbacks. Even after the initial manipulation, positive feedback loops should be associated with sustained changes in individual behaviour over time, whereas negative feedback loops should be associated with individuals returning to their original, pre-manipulation behaviour (and state). If the model makes predictions on how mediating factors (e.g., local density, risks, or resources) should affect personalities on an ecological time scale, experimentally manipulate these mediating factors.

Take feedback loops into account when planning data collection and statistical analyses. Empirical studies often treat some of the state variables described above as nuisance parameters, and try to correct for these, potentially removing the signature of feedback loops from the data. We thus suggest that empiricists should not follow the common practices of standardizing the social environment experienced by individuals, or to statistically standardize

for individual body size or energy state when assessing individual behavioural variation.

Ideally, collect longitudinal datasets, measuring individuals' state and behaviour repeatedly over relevant time scales (i.e., time series). We next describe statistical methods for quantifying feedback loops and their outcomes.

Quantifying within-individual loops

In principle, feedback loops can be characterized as an individual property, and thus vary among individuals [57]. For testing within-individual feedback loops, repeated measurements of individuals' behaviour and state are essential. Statistically, feedbacks within a single individual can then be captured with a 'double' phenotypic equation where behaviour ($y_{t,b}$; b for behaviour) and state ($y_{t,s}$; s for state) at time t are both response variables (Box 3). The key difference with classic phenotypic equations [58,59] is that some variables are both predictor and response.

Within-individual feedback loops leave various traces in empirical data when captured in action. First, among-individual variation in state and behaviour should increase over time with positive feedback and result in positive correlations between individual intercepts and slopes of temporal reaction norms ('fanning-out'; left and middle panels of Figure 2A,D). When the effect of (current) state on (current) behaviour ($\lambda_{s \rightarrow b}$) and (current) behaviour on (future) state ($\lambda_{b \rightarrow s}$) are both positive (Figure 2D, right panel), state and behaviour shift in the same direction within the same individual, causing positive 'within-individual correlations' [60]. When $\lambda_{s \rightarrow b}$ and $\lambda_{b \rightarrow s}$ are both negative, state and behaviour shift in opposite directions, causing negative within-individual correlations (Figure 2A, right panel). Along the same lines, negative loops also leave distinct patterns of (co)variance, for example, negative intercept–slope correlations ('fanning-in'; left and middle panels of Figure 2B,C). Parameters $\lambda_{s \rightarrow b}$ and $\lambda_{b \rightarrow s}$ can also be estimated directly, for example, using structural equation modelling (Box 3).

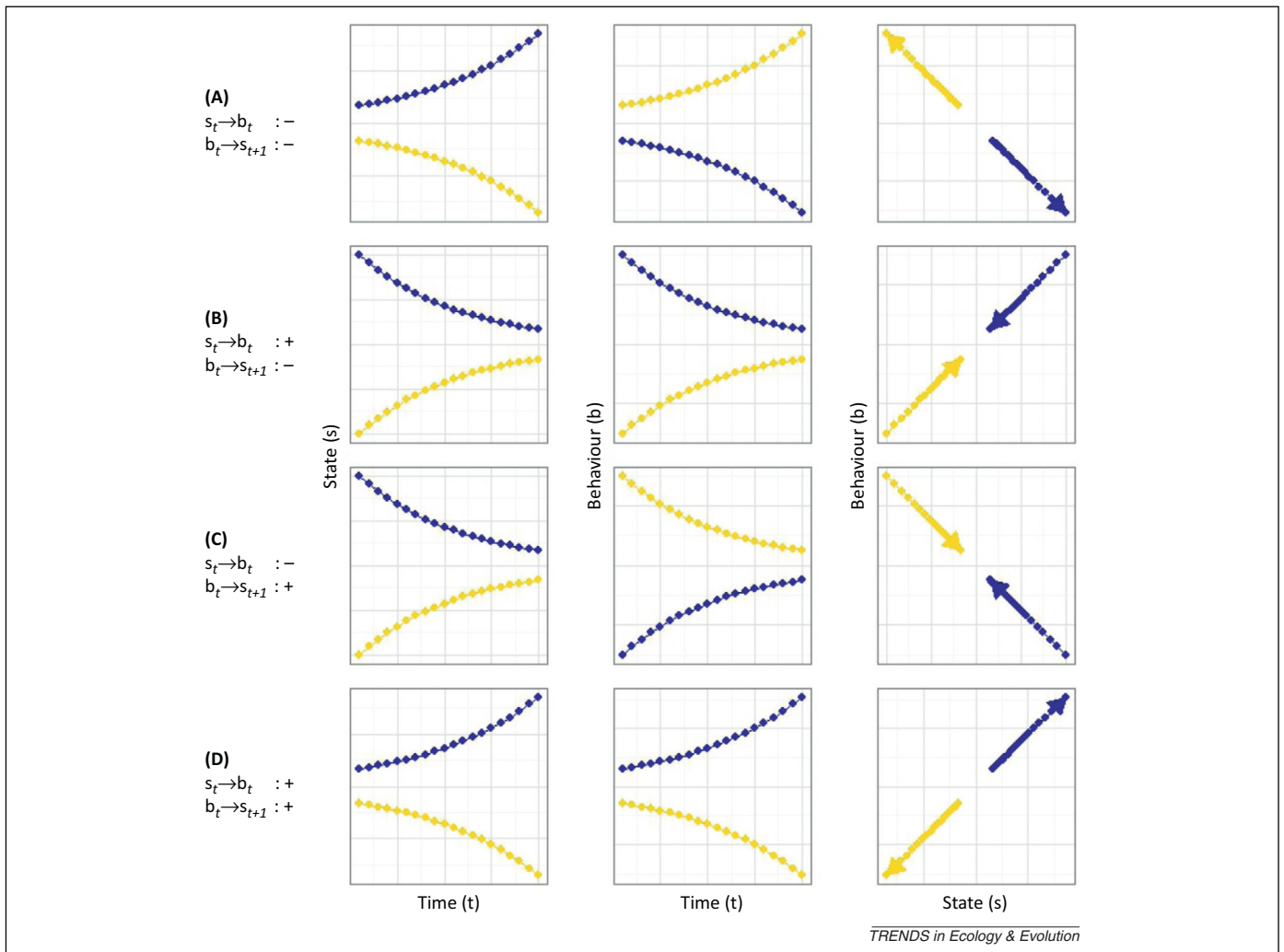


Figure 2. Patterns of variation in temporal reaction norms for state (s) (left panel) and behaviour (b) (middle panel) while within-individual feedback loops are 'in action'. All scenarios are drawn from the simple equations given in Box 3, with starting values of 0.1 (blue individuals) and -0.1 (yellow individuals) for state at time t for 20 time steps. Scenarios A through D differ in values of $\lambda_{s \rightarrow b}$ and $\lambda_{b \rightarrow s}$ ('-' = -0.3; '+' = +0.3), resulting in either positive (A,D) or negative (B,C) loops. Different scenarios come with specific predictions for pattern and direction (arrows) of within-individual covariance in state and behaviour leading to within-individual correlations while feedback loops are 'in action' (right panel). We note that negative feedback can, depending on parameter settings, also result in cycling or chaos; those scenarios are not depicted but would not result in among-individual differentiation (state-dependent personality).

Individual divergence due to positive feedback would typically cease at some point in time either because of biological floors or ceilings to both state and behaviour, because behaviour is open for modification only during certain developmental stages [9] or because the effect of state on behaviour (or vice versa) is non-linear. At such 'end stages', within-individual correlations would decrease to zero and be replaced by stable 'among-individual correlations' [60].

Quantifying among-individual feedback loops

Positive within-individual feedback loops lead to within-individual covariance between state and behaviour while the loop is in action. Among-individual correlations represent the final outcome of this process (i.e., stable, state-dependent personality differences); these among-individual correlations are, notably, of non-genetic origin. However, feedback loops can also occur at longer (evolutionary) time scales, and thus result in among-individual correlations due to the evolution of genetic correlations between the heritable

parts of state and behaviour. On such an evolutionary time scale, long-term experiments could be used on short-lived organisms to quantify joint changes in breeding values of behaviour and state over multiple generations. Similarly, phylogenetic analyses comparing populations or species could be used to study the joint evolution of state and behaviour. Provided that feedbacks are indeed a function of ecological condition, a final approach would be to compare genetic correlation structures across populations (or species) experiencing different ecologies.

Concluding remarks

In this paper, we highlighted a parsimonious explanation for state-dependent personality due to positive feedbacks between state and behaviour. We reviewed theoretical models on the role of feedback loops in shaping behavioural variation both within and among individuals. The models discussed in this paper indicate that the direction and strengths of feedback loops will often depend on the ecological conditions. We clarify that positive feedback

Box 4. Outstanding questions

- **Feedbacks and distribution of personality types.** Feedbacks would, in their simplest form, result in dichotomous among-individual variation in behaviour (see Figure 2 in main text), hence discrete personality types. What are the mechanisms that prevent the emerging among-individual variation to become dichotomous? What is the timescale over which feedback loops act? Is there an end-point to positive feedback and why? At what developmental stages do feedback loops exist, and why?
- **Selection on feedback loops.** Feedback loops imply that state is a function of behaviour and vice versa. Such functions are commonly viewed as reaction norms [58,72]. Do individuals differ in state-behaviour and behaviour-state reaction norms, whether in intercepts or slopes? And are components of these reaction norms correlated? How does selection act on these reaction norms (Box 1).
- **Ecology of feedback loops.** Are feedback loops a function of ecological conditions (e.g., competitive regimes, predators, food availability), and if so, which ecological factors are of key importance? Can temporal or spatial variation in ecological conditions explain variation among individuals in magnitude and sign of feedback loops?
- **Which combinations of behavioural and state variables show feedback?** Theory has been developed for specific combinations of states and behaviours (see Table 1 in main text). How general are the associated predictions? Do they apply to specific behaviour-state combinations or more generally?
- **Ecological versus evolutionary time scales.** Feedbacks can occur both within single individuals and across individuals, leading to among-individual correlations of non-genetic versus genetic origin, respectively. When should feedback loops evolve at each of those time scales? Do feedback loops differ between time scales; if so, why?
- **Fitness consequences of state-behaviour feedbacks.** Do positive (divergent) feedbacks generate among-individual differences in fitness, or do they produce alternative state-behaviour combinations with equal fitness, and under what conditions? Does the strength or direction of the feedback loop predict changes in individual fitness proxies through time?

loops can lead to adaptive personalities (among-individual covariance between state and behaviour) whether of genetic or non-genetic origin. We further provide guidelines for empirical testing of adaptive theory (Box 3). We hope our conceptual framework for explaining variation in personalities proves useful for guiding future integration of theoretical and empirical work in this exciting field with many outstanding questions (Box 4) to be addressed in the near future.

Acknowledgements

We gratefully acknowledge stimulating input by Caitlin McGaw, and participants of the Symposium 'Personality: causes and consequences of consistent behavioural variation' funded by the Volkswagen Foundation. We thank Anne Rutten for drawing Figure 2 based on the double phenotypic equation presented in Box 3. M.M. and N.J.D. were funded by the Max Planck Society. K.J.M. was funded by a Natural Sciences and Engineering Research Council of Canada postdoctoral fellowship and the Max Planck Society. M.W. was funded by the B-Types research project (SAW-2013-IGB-2) through the Leibniz Competition. A.S. was funded by National Science Foundation grant IOS 0952132, and P.O.M. was funded by a postdoctoral fellowship from the Fonds de recherche du Québec – Nature et technologies.

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