Evaluating measurement models in animal personality: operational, latent variable and network approaches

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Abstract

Animal personality is the study of consistent individual differences in behaviour. Underlying this innocuous definition, however, is a history of diverse scientific ideas and terminological confusion that continues to elicit debate about the usefulness of personality in animal behaviour. This review connects these debates to the absence of a unifying *measurement model* for animal personality. A measurement model is a blueprint for how theoretical constructs and observed variables relate to each other, and thus makes the assumptions of scientific theories explicit. The field of animal personality is demonstrated to employ two predominant measurement models, *operational* and *latent variable*. Each framework harbours its own conceptual problems that are shown to contribute to debates about animal personality. Five requirements for a suitable measurement model for animal personality are subsequently provided. The review ends by considering the utility of the *network* approach arising in human psychology as an alternative measurement framework for animal personality.

1 Introduction

Over the last two decades, individual differences in behaviour has become a dominant research paradigm in animal behaviour. Widely referred to now as *animal personality*, evidence that individuals differ relatively consistently in their behaviours from others is of interest to a range of scientists in evolutionary and behavioural ecology, animal cognition, behavioural physiology, and applied animal welfare science. Beyond recording consistency in individual behaviours within populations (e.g. risk-taking [1]), animal personality research is concerned with the non-trivial questions of whether behavioural consistency is an evolutionary adaptation or constraint [2, 3, 4], the relative importance of genetic compared to situational factors in maintaining behavioural consistency [5], why organismal behaviour appears globally organised into correlated

suites of traits (i.e. *behavioural syndromes*; [6]), and why similar behavioural dimensions are found in diverse taxa [7, 8].

30 The rise of animal personality has not been without contention, however, with a number of papers attempting to clarify the personality concept [9, 10, 11, 12, 13], particularly in its distinction from human personality psychology, or even questioning the value of animal personality as a science [14, 15]. Proponents of personality highlight the importance of behavioural consistency, more precisely behavioural *repeatability* (the fraction of total behavioural variance attributable to between-individual differ-
35 ences; [16]), in its own right and how it relates to the heritability of phenotypic traits of interest in quantitative genetics [5, 11]. The criticisms levelled against personality have included claims that it is overly anthropomorphic [15], with terminology serving only to increase media accessibility [14], or that the field brings no new insights about animal behaviour beyond what can be inferred by more established disciplines
40 [14, 17, 15]. Others have identified a lack of conceptual cohesiveness between personality studies [12], or addressed the need for more hypothesis-driven frameworks for understanding behavioural repeatability [18, 19]. While rebuttals to these criticisms have rightly indicated that personality studies have spawned a new form of individual-oriented research in fields like behavioural ecology [20, 21], it is clear that
45 across animal behaviour, personality remains a controversial topic.

The goal of the present review is not to contribute to the confusion about animal personality, but instead to highlight a broader cause of this dissension: that animal personality science has no unified *measurement model*. A measurement model is a theoretical device that links unobserved variables to observed variables [22, 23, 24],
50 and provides a blueprint for scientific theories [22]. Human psychologists devote an entire area to the question of psychological measurement — *psychometrics* — but what it means to measure something in animal behaviour has not received the same level of focus. Regardless of which side researchers align with on the contention about animal personality, there has been a consistent call for more theoretically-
55 justified and hypothesis-driven personality research focused on the mechanisms and adaptive significance of repeatable individual differences [11, 25, 26, 27, 28, 19, 29, 14, 12, 30, 31, 32]. It is argued here that defining a clearer measurement model for animal personality, specifically the relationship between personality traits, observed behaviours, and behavioural repeatability, will greatly enable this endeavour.

60 Section 2 discusses the dominant definition of animal personality and personality traits from behavioural and evolutionary ecology as any observable behaviour that is repeatable [11], which aligns with an *operationalist* measurement model. After raising well-known conceptual problems that operationalism induces, section 3 reviews the *latent variable* approach to personality. Latent variable modelling has been used in
65 human psychology for over a century, and thus the field has learned of the problems with this form of measurement model, both in theory and in practice, that are infrequently discussed in animal personality. Lastly, the final section examines what an ideal measurement model in animal personality needs to provide, and investigates the

utility of an alternative *network* approach that has risen within human psychology
 70 over the last decade [33, 34, 35, 36], and has recently been used in animal behaviour
 [37, 38]. It is important to note that this review does not intend to equate animal
 personality with human psychology, nor does it ignore the unique history animal
 personality science has in its own right [39, 21]. Instead, it illustrates the common
 conceptual problems faced by both fields, irregardless of their differences, as empiri-
 75 cal sciences grappling with the difficult task of measurement, and motivates a deeper
 appreciation of measurement in animal personality to provide a more constructive
 foundation for discussing theoretical issues in the future.

2 The operational approach

Individual variation in behaviour is a core tenet of evolutionary biology, but the pro-
 80 posal that individual variation may be adaptive has only gained widespread traction
 in the last two decades [1, 40, 6, 41, 3]. This is not to imply that individual variation
 in behaviour was not of interest before this time, however. Psychologists, ethologists,
 stress physiologists, applied animal behaviourists and others had in fact been writ-
 ing on the presence of individual variation in behaviour and ‘personality’ for decades
 85 [42, 43, 44, 45, 46, 47, 48, 49, 50, 51, 52]. In large part, these studies were a direct
 analogue to studies of human personality because the goal was to examine whether
 animals showed similar personality trait structures to humans [52]. The hypothesis
 that individual variation may be adaptive, rather than just noise around an adaptive
 peak, was also discussed in evolutionary biology 40 years ago [53, 43]. This was a
 90 timely extension in using “natural selection to explain differences between organisms
 at increasingly finer scales” [40, p. 199].

The introduction of animal personality into studies of behavioural and evolution-
 ary ecology at the scale seen today was greatly facilitated by Reale *et al.* [11]’s
 seminal article, which operationalised personality (referred to as ‘temperament’ in
 95 the article) in terms of purely observable behaviours. Whereas psychologists referred
 to personality traits as latent psychological properties of individuals, Reale *et al.* [11,
 p. 294] defined animal temperament as “the phenomenon that individual behavioural
 differences are consistent over time/across situations”, and proposed five initial traits
 that most behaviours reflect (aggression, sociality, boldness, exploration and activity).
 100 Rather than interpret these traits as “‘unobservables’ or qualities that are difficult to
 measure (e.g. dispositions)...[that] may restrain ecologists and evolutionary biologists
 from studying temperament” [11, p. 294], the authors emphasised that “each trait
 should be operationally defined and its ecological validity tested” (295). Importantly,
 this definition of personality is a *population-level* phenomenon, and not something
 105 that exists at the level of individuals.

The distancing of animal from human personality was reinforced by subsequent
 authors [9, 10, 20]. For instance, Carter *et al.* [10, p. 468] wrote that the term ‘trait’
 “is used in behavioural ecology to mean a measurable aspect of an individual’s be-

110 haviour that is, usually, repeatable while in psychology the use is more abstract and describes a construct". Bell [20, p. 626] further emphasised that behavioural ecologists do not infer any higher-order cognitive processes underlying personality: "We are agnostic about the sources of variation...and how long the differences endure". Operationalising animal personality as any measurable behaviour that is repeatable allowed integration to established concepts and statistical formulations in quantitative genetics. Notably, the variance of between-individual differences in behaviour is 115 equal to the sum of additive, permanent environmental and genetic dominance variance [5]. From the definition of heritability as the ratio of total genetic variance to phenotypic variance (broad sense) or the ratio of additive genetic variance to phenotypic variance (narrow sense), behavioural repeatability was defined as the ratio of 120 between-individual variance to total phenotypic/behavioural variance. Repeatability is readily calculated from the variance components of hierarchical statistical models [16, 54].

The operational approach has no doubt been a powerful empirical paradigm for quantifying individual variation in behaviour. Its use of hierarchical statistical 125 modelling has also integrated personality with the concepts of behavioural plasticity [55] and predictability [56, 57], continuing the expansion of understanding how natural selection maintains behavioural variation across multiple hierarchical levels [40, 58, 59, 29, 60, 61]. This has been concomitant with a shift in behavioural ecology study design to collecting repeated measures of often multiple different behaviours 130 [21]. Nonetheless, personality in behavioural and evolutionary ecology has received criticism, including that the term personality continues to invoke anthropomorphic interpretations of behaviour [15], and that studies quantifying behavioural repeatability are overly descriptive [25, 14, 18], resulting in statistical estimates of behavioural repeatability with little explanatory value.

135 For instance, there are few guidelines about what constitutes sufficient behavioural repeatability to be evidence of personality. Variance components, and thus repeatability, can never be exactly zero, making finding a suitable null hypothesis difficult [14]. There is also a lack of theoretical rationale for why different values of repeatability are found [18]. Despite some theoretical models explaining when individual 140 differences should evolve [26], those models do not make numerical predictions about the repeatability coefficients in particular. While repeatability is often around 0.35-0.4 [62], *a priori* numerical predictions of repeatability beyond this moderate value are rare to come by. Indeed, because repeatability frequently accounts for less than 50% of behavioural variance, there are questions of how much emphasis should be 145 placed on repeatability for predicting behaviour [63]. Quantifying repeatability, and labelling repeatable behaviours with terms such as boldness or exploration, has thus motivated some to question the worth of personality at all [14].

The aforementioned criticisms could rightly be made about many different fields of empirical research, and some valid responses to these criticisms have been provided 150 [21, 39, 20]. However, a broader reason driving such criticisms becomes evident when

one assesses the type of measurement model the operational approach defines: the operational approach is a re-emergence of *operationalism*, the now-rejected philosophy of science originating in the 1920s with Bridgman's 1927 book *The Logic of Modern Physics*. Bridgman proposed that theoretical constructs are synonymous with the methods used to measure them:

To find the length of an object we have to perform certain physical operations. The concept of length is therefore fixed when the operations by which length is measured are fixed: that is, the concept of length involves as much as and nothing more than the set of operations by which length is measured.

- Bridgman [64, p. 5]

At a time when psychological testing (e.g. to predict educational attainment) was rampant under the logical positivist and verificationist movements, human psychologists promoted operationalism because it allowed the “illusion of control over the perplexities of the ‘real world’ ” [65, p. 150] by reducing theoretical ideas (e.g. intelligence) to observables (e.g. scores on intelligence tests). As Stevens [66, p. 323] wrote, this “ensures us against hazy, ambiguous and contradictory notions and provides the rigor of definition which silences useless controversy”.

Early commentators on the rise of operationalism in physics [67] and psychology [68] explicated its problems, and philosophers and psychologists have continued to publish on its problems as a philosophy of science throughout the decades [69, 70, 71, 22, 72]. The ‘tragedy of operationalism’ [73] is that it equates meaning with measurement [69], rendering scientific constructs ontologically ambiguous [22]. To say that the concept of length is defined by the methods used to measure it automatically means that every different method used to measure the length of an object, including two different people or the same person at two different times, necessarily results in a different length concept [69, 22, 23]. Moreover, operationalism revokes the idea that one measurement can be ‘better’ or ‘worse’ than another, because both measurements are equally synonymous with the construct under study by definition [69]. Concepts such as validity and reliability thus fall by the wayside under operationalism [23]. In terms of measurement models, operationalism provides no such thing [74]: equating the theoretical construct with the observed measurements absolves the need for the construct entirely.

In practice, most scientists would find the operationalist doctrine, taken to its logical conclusion, nonsensical. Indeed, the logical positivists removed support for operationalism once its problems were revealed, and even Bridgman relaxed his ideas in later years [69, 71]. Scientific constructs cannot be exhausted by their operational definitions [72] because at some point the concept has to be distinguished from the methods or operations employing it [69, 73]. Borsboom [22] has discussed the problems operationalism has incited in psychology's classical test theory, and in the common practice of operationalising theoretical attributes and using the measures

Figure 1: A schematic representation of the ‘tragedy of operationalism’. Imagine a single personality trait, P , which is operationally defined (solid lines; O_i , from $i = 1, \dots, \infty$) by different observed behaviours ($\mathbf{B} = \{B_i\}$, from $i = 1, \dots, \infty$). Operational definitions synonymise the personality trait with each observed behaviour, precluding understanding the causal relationship between P and measures B_i (e.g. $P_i \rightarrow B_i$ or $P_i \leftarrow B_i$) or allowing inference of how a single personality trait may influence all behaviours (e.g. $P \rightarrow \mathbf{B}$). Due to an infinite number of ways of measuring behaviour, there are also an infinite number of concepts (indicated by P_∞) instantiated operationalism.

as *synonymous* with those attributes [74]. Outside psychology, Stafleu *et al.* [75] remark that operational approaches have eroded the concept of animal welfare of its ethical aspects. There is, furthermore, close relationships between common methods of assessing validity, such as construct validity, and operationalism, which have also been highly criticised [76, 23].

Defining personality directly in terms of behavioural repeatability is another instantiation of operationalism. Indeed, Reale *et al.* [11]’s support for operationally defining traits to avoid eliciting notions of psychological dispositions shares significant similarities with the reasoning for adopting operationalism in psychology discussed above. It is crucial to recognise that this is not a claim that behavioural repeatability is a-theoretical, or that its importance to understanding patterns of behavioural variation in behavioural and evolutionary ecology (e.g. [59, 60, 58]) should be ignored. It is a claim that making behavioural repeatability *sufficient*, and not simply *necessary*, to define animal personality is another demonstration of operationalism. This idea is shown schematically in graph-theoretic form in Figure 1. Here, an infinite number of behaviours are bound (thick black lines) to separate personality traits, with no way of determining the relationship between traits nor the causal relationship between traits and behaviours (i.e. it is intentionally *not* a directed graph).

Arguments that personality in behavioural and evolutionary ecology has resulted in a literature that is too descriptive, or that there is a need for more hypothesis-driven approaches [18, 19], is a function, I argue, of the more general problem of operationalism: if repeatability is sufficient to define a personality or trait, then nothing more is required of researchers than to estimate repeatability. That the field of personality has too many descriptive studies, with apparently meaningless trait vocabularies

tacked on [14], is no surprise if the dominant measurement concept is operationalism. Assessing validity and reliability cannot ameliorate these matters, as has been argued previously [10], because operationalism obfuscates any notion of more than one measure of the same construct, or even of two different raters measuring the same construct [22, 76]. By extension, operationalism distorts our understanding of behavioural correlations, or behavioural syndromes, because every correlation between two repeatable behaviours must in fact represent an among-individual correlation between two different traits or a syndrome. There are an infinite number of ways we can measure behaviour, and therefore there must be an infinite number of behavioural syndromes if operationalism is to be adhered to.

Wanting to link repeatable behaviours to higher-order behavioural dimensions, on the one hand, and following an operationalist approach, on the other, causes conceptual tension that is seen in empirical research. One example is highlighted by Dochtermann and Nelson [77], who found that two measures of exploration were repeatable but, unexpectedly, uncorrelated. The authors comment that the lack of predicted correlation “makes determining whether ‘exploratory behaviour’ is generally a trait problematic” [77, p. 1115], and they suggest that more attention should be placed on understanding what traits are, as they have been in human personality psychology. In this instance, the operational definition has eliminated any inferential power to make sense of the lack of clear correlation between behaviours. One cannot conclude that exploration is *not* a trait, because both behaviours meet the requirement for exploration under the definition of behavioural repeatability, and are ecologically valid. Yet, at the same time, the evidence does not support that exploration *is* a trait because the absence of a significant correlation between two ecologically connected behaviours contradicts the pragmatic notion that traits can be measured by multiple behaviours. To enable a clearer conclusion would require an explicit measurement model of personality that distinguishes between exploration, as an unobserved variable quite separate to scientific practice, and the *measures of* exploration, as indeed the authors indicate later in their article.

Operationalism provides no clear measurement model for personality science, and I have argued that this has been a driving force in fueling debate between personality researchers. Importantly, this argument is agnostic to the fact that behavioural repeatability and animal personality is motivated from evolutionary biology, whereas human personality is motivated by notions of psychological dispositions [11]. Therefore, claims that criticisms of animal personality misleadingly ignore these disciplinary differences [39] do not apply. The remedy to operationalism is to align with a philosophy of science and measurement approach that allows distinguishing the concept from measurements of that concept.

3 The latent variable approach

Animal personality researchers already have a more suitable measurement model than operationalism in their toolkits. Alongside calculating behavioural repeatabilities using hierarchical statistical modelling, another approach to studying personality involves collecting multivariate data on behaviour and explicitly decomposing the variance into underlying behavioural dimensions [78]. Note that this approach is immediately at odds with an operationalist definition by introduction of unobserved variables into the measurement process. This *latent variable* modelling offers a principled statistical methodology for relating unobserved or latent variables to observed or manifest variables [79]. Beyond its data analysis applications, latent variable models also provide a principled method of thinking about the measurement relationships between variables, such that theoretical relationships can be tested [22]. Latent variable models have, consequently, been a mainstay of human psychology for over a century [80, 81], including personality psychology, for inferring latent psychological constructs from observed measurements, such as the infamous Five Factor Model of human personality [82]. Moreover, early applications of personality to animal behaviour by comparative psychologists, ethologists and applied animal behaviourists used latent variable models [47, 42, 49].

In recent years, latent variable modelling has also increased in popularity in behavioural ecology to characterise personality traits and behavioural syndromes [7, 83, 84, 29, 85, 32]. Therefore, despite differences between human psychology and animal behaviour in studying personality, there appears to be a convergence in methodology to using latent variable modelling [29]. However, whereas latent constructs in human personality have been expressed as real, biological variables [82], there has been a stark lack of discussion in animal personality over *what* latent traits derived from latent variable models refer to in animal behaviour, or whether latent variables are causal variables or composite variables with no causal status (although see [29]). As is known from human psychology, both these problems cause confusion about what personality and personality traits refer to. For example, latent variable modelling results in processes of ‘verbal magic’ [86] when naming latent factors, and unclear causal relationships between latent and manifest variables results in model misuse [74].

Latent variable models generally come in two different flavours depending on the causal relationships they indicate between latent and manifest variables, as shown by the directed acyclic graphs in Figure 2. Formative models, most commonly employed as principal components analysis, assume that the latent variables are caused by changes in the manifest variables (Figure 2a). Reflective models, most commonly employed as factor analysis for a continuous latent variable, assume that variation in the manifest variables are caused by changes in the latent variable (Figure 2b). There are no assumptions that manifest variables should be correlated with one another in formative models [79], but manifest variables should be conditionally indepen-

Figure 2: Formative and reflective latent variable models, adapted from Bollen & Lennox [79]. Formative models assume the latent personality trait is composed of a linear combination of perfectly-measured manifest behavioural variables (i.e. $\sum_i^P \beta_i B_i$). The manifest variables represent only a subset of (possibly covarying, i.e. $\rho_{ij}, i \neq j$) variables that could compose the latent trait, so the latent trait is measured with error (σ). Reflective models assume that variation in the manifest variables are caused by changes in the latent personality trait (i.e. $\sum_i^P \lambda_i x$, where x is the latent variable). The manifest variables are not completely described by variation in the personality trait, and so can be measured with error (ϵ_i), and are assumed conditionally independent given the latent variable.

295 dent given the latent variable(s) in reflective models. Authors in human psychology [87, 79, 88, 89, 74] and some now in animal behaviour [78, 84, 90] (see also [91]) have recognised the continued conflation of these opposing models, not helped by inconsistent language in popular statistical analysis software [74]. It is not just potential differences in the statistical results that are important (e.g. [89, 90]; but see [92, 93]),
300 but that the causal status of the latent variables are frequently ignored [94]. This necessarily increases confusion over what latent variables represent when discussing animal personality.

For the most part, psychologists agree that psychological constructs, like personality traits, are best viewed as reflective latent variables [22, 94, 86, 87, 95]. Such a
305 view necessitates a *realist* interpretation of traits — that is, traits are real biological variables distinct from the methods and procedures of scientific practice [22, 72, 86]. This purview is most powerful within a confirmatory paradigm, because the causal hypothesis of the latent variables allows us to test certain assumptions using reflective latent variable statistical models. For example, confirmatory factor analysis or, more
310 generally, structural equation modelling can be used to test the assumptions of *local independence* [96] and *measurement invariance* [97, 98, 99, 100]. Local independence states that manifest variables are conditionally independent given the latent variable, meaning accounting for the latent variable in the directed acyclic graph of Figure

2b should ‘screen off’ any correlations between the manifest variables. Formally, the probability, π , of two manifest variables, $B_{1,2}$, given a latent variable, should be factorisable as $\pi(B_1, B_2|P) = \pi(B_1|P)\pi(B_2|P)$. Measurement invariance is, by contrast, the assumption that any differences between groups (e.g. populations, individuals, experimental groups) are functions of differences in the latent variable rather than in other aspects of the measurement relationship. Formally, given some specific value of a latent variable, P_x , and two different groups, $G_{1,2}$, measurement invariance implies that $\pi(B|P_x) = \pi(B|P_x, G_{1,2})$. If measurement invariance does not hold, then there must be *other* processes going on in the measurement process that affect the observed behaviours, and one cannot infer that group differences are functions solely of the latent variable [22]. Differences between majority and minority ethnicities on intelligence tests may not be a function of underlying intelligence, for example, but due to differences in reading comprehension related to language abilities [101].

The application of latent variable modelling in animal personality is less regulated and rigorous than its application in human psychology and psychometrics, despite calls for their better use [78, 90]. Although reflective models are used by a number of researchers [83, 84, 60, 85], there has been too little discussion about the *a priori* justification, or lack thereof, of choice of formative (particularly principal components analysis) and reflective models in animal personality [78]. Assessments of measurement invariance and local independence, despite a number of studies comparing traits across species, populations and contexts, are sorely lacking (but see Goold & Newberry [102]).

One exception worth examining is that of Araya-Ajoy and Dingemanse [29], who provide a framework for investigating latent behavioural ‘characters’ using a two-step multivariate hierarchical regression and structural equation modelling approach. The authors clearly outline the assumptions a latent variable interpretation of behavioural characters imposes, such as that correlations between behaviours should be similar in different contexts and environments if in fact a latent variable is causing behaviour. Despite this, the authors provide no reference to the already long history of testing these assumptions in latent variable models in human psychology, namely local independence and measurement invariance. The authors further state that their proposed methodology has not been “fully embedded in human personality research” [29, p. 8], particularly with respect to modelling between- and within-individual correlations. This is in fact false: human psychologists have proposed a variety of tools based on structural equation modelling that can estimate between- and within-individual variation in latent and/or observed variables across time and contexts, such as dynamic factor analysis [103] or state space models [104]. These methods allow for different assumptions to be tested within the same statistical model, rather than the two-step approach presented by Araya-Ajoy and Dingemanse [29].

Latent variable modelling has, therefore, untapped potential to offer personality researchers in animal behaviour to test explicit theoretical hypotheses about how observed behaviours are caused by unobserved, latent traits or characters [102]. As-

certaining local independence and measurement invariance could offer new avenues for testing the comparative structure of personality across species (i.e. do the same measurement relationships hold in different species such that the same trait can be inferred across species). Validation of personality assessments can also make use of latent variable modelling in line with modern psychometric ideas [76, 94], rather than relying on inspecting patterns of inter-correlations between variables [10]. This is not an argument for more advanced statistical models, but motivation for making measurement relationships between unobserved traits and observed behaviours explicit.

3.1 Problems with latent variables

The latent variable approach provides a more principled measurement model for understanding personality and personality traits. It is worth addressing, however, some pressing concerns about latent variables that have been raised in human psychology. Namely, if latent variables are to be interpreted in a realist sense, where is the evidence supporting the idea of homogeneous, ‘functional units’ [29] in biology?

If latent variables are real, biological variables, they presumably must exist at the level of individuals. However, most studies applying latent variable models do so at the population level, rather than imposing a hierarchical structure where estimation of the latent variables varies across subjects. For example, Molenaar [105] demonstrated that the Five Factor Model of human personality, considered a ‘universal structure’ of psychology [82], does not hold for within-subject data [104]. This is a generalisation of the ecological fallacy [106, 107], and arises because behaviour is ‘non-ergodic’ [105, 108], meaning the average value across a set of units (e.g. animals) does not equal the average of repeated realisations of each individual unit. Although Araya-Ajoy and Dingemanse [29] proposed a hierarchical structure for behavioural variation that includes latent behavioural characters, the latent variables were still estimated at the population level. Thus, there have been no applications of the hierarchical latent variable models as proposed by Molenaar [105] in animal personality. Employment of such modelling schemes would more rigorously test whether latent behavioural traits or characters hold at the individual level.

If a within-individual interpretation of latent variables is permitted, latent variables still appear to be an inaccurate interpretation of the biological mechanisms underpinning behaviour. A notable example is general intelligence, also known as the *g*-factor. Despite over a hundred years of research on *g*, a homogeneous biological *g* is yet to be found [109, 110, 111]. Brain networks underlying intelligence and other cognitive functions vary across people and contexts [112, 113], and are dynamically-distributed across the brain [114]. This emerging evidence questions the functional modularity of the brain [115, 116] and suggests that *i*) the same biological structures have multiple different functions, known as degeneracy, and *ii*) different biological structures have similar functions, known as redundancy [117, 118, 119]. Representing complex mechanisms by the relatively fixed structures of latent variables is to com-

mit the ‘fallacy of misplaced concreteness’ [120], a prominent source of confusion that has been identified as distorting empirical progress on concepts as wide-ranging as human intelligence [121], forest biomass [122], and economic equilibrium [123]. It is also to take out a ‘loan on intelligence’ [124], by equating unobserved processes with
400 brain-based, cognitive processes without sufficient evidence.

Latent variable models will likely continue to be a dominant measurement model despite problems with the realist interpretations of latent variables. However, there are alternatives to latent variable perspectives. In the final section, I will outline the requirements for an ideal measurement model for animal personality based on the
405 preceding discussion, and take a brief look at the rising network approach in human psychology that has been proposed as an alternative paradigm to latent variable models.

4 Alternative measurement models for animal personality

410 The discussion above relates more generally to the growing call for explicit theoretical models to drive hypotheses in empirical science. Theoretical models encode causal hypotheses of how complex systems function [125, 126], and encourage more reproducible science by facilitating practices such as pre-registration [126]. Golonka and Wilson [127] argue for a better ‘guide to discovery’ in human psychology based on
415 clearer theoretical roadmaps. Theoretical models of how behavioural variation and, thus, animal personality evolves do exist [26, 4, 128, 129, 130]. However, there is a disparity between these models and the majority of personality studies that rely on quantifying behavioural repeatability alone, or fitting a latent variable model with few of the checks and balances required to validate a latent variable interpretation of
420 behaviour [94]. There is also a disparity between recognition of the complex genetic, physiological and neurobiological mechanisms underlying traits [11], and the types of measurement models employed.

4.1 Measurement model requirements

Five requirements for a measurement model in animal personality can be inferred
425 from the preceding sections. The measurement model must ideally:

1. Reference both the theoretical construct and the observed variables
2. Apply to individuals, and not aggregates (e.g. populations)
3. Encode a causal hypothesis about how observed behaviours are expressed
4. Be dynamic, based on time and/or context-varying influences

- 430 5. Allow for the inclusion of how other variables, such as biological and environ-
mental factors, influence focal behaviours

The operational approach excels at evaluating the time- and context-varying aspect of behaviour (requirement 4) by virtue of its use of hierarchical modelling, and such models can also include predictors of individual variation (requirement 5) as
435 observation- and/or individual-level independent variables [54, 55]. Operational approaches do not, however, make explicit reference to theoretical constructs due to synonymising personality traits with observed behaviour, precluding any causal hypotheses about the generative processes of behaviour. Behavioural repeatability, moreover, only exists at the level of the sample and not individuals.

440 Latent variable models at first seem to be able to meet all the five requirements, but as discussed in the previous section the major argument against their use is that the causal hypothesis they impose (i.e. that homogeneous latent variables cause behaviour) has largely not been borne out by empirical research. In animal behaviour, for example, while mechanisms of behaviour might be broadly categorised into units
445 (e.g. HPA-axis, cognitive abilities), these mechanisms are in fact complex structures in their own right. The physiological system is, for example, a network that acts as an integrated whole, rather than composed of independent markers dictating behaviour [131]. It would be useful to have a measurement model that reflected this complexity.

Theoretical models of the evolution of individual differences in behaviour also
450 do not easily align with either operational or latent variable measurement models. So-called state-dependent models [128, 129, 130] are commonly used to describe behavioural consistency, the idea being that behavioural stability is caused by stability in an endogenous (e.g. energy reserves) or exogenous (e.g. predation risk) ‘state’. State-dependent models, therefore, apply to individuals and not just populations,
455 meaning additional information would be required to link state dependency producing individual behaviour, to the population-level construct of behavioural repeatability. State-dependent models also raise an important concern with latent variable models: states and behaviours demonstrate positive feedbacks [130] such that small differences in initial states between individuals could lead to large differences in states
460 and behaviours in the future. Such positive feedbacks are not easily encoded in common latent variable models (Figure 2) [35]. Multiple states may also impact the same behaviours, and the same state may impact multiple behaviours, leading to the degeneracy/redundancy issue discussed earlier that is inadequately handled by latent variable models. In the following section, a novel measurement model based
465 on networks from human psychology is reviewed, which could provide a unifying measurement framework for animal personality.

4.2 The network approach

Multiple areas of scientific inquiry have converged upon a network view of complex systems, such as evolution, communication systems, physiological and neurobiological

Figure 3: A hypothetical individual-level network of behavioural variables (squares labelled B_i) clustering into two emergent ‘traits’ (yellow and blue squares). Each behaviour has a within-behaviour effect through time/across contexts (self-directed loops denoted ρ_i), and between-behaviour causal effects (directed arrows denoted β_i). Dashed lines represent causal effects between traits.

470 systems, and developmental systems [132, 131, 133, 114, 134, 135, 136]. This is not only due to the utility of network statistical models, but reflects a realisation that systems are composed of multiple interacting entities that frequently show non-linear and emergent behaviours [135]. Philosophers have also revived interest in process-based philosophies of science [120, 137, 138] that assert that the natural world, including animal behaviour [139], is not composed of fixed substances or ‘things’, but self-maintaining processes that re-emerge through time (“enduring things are never more than patterns of stability in a sea of process” [137, p. 14]). A network perspective is a natural representation of processes (e.g. microbiology; [140]).

480 Can behaviour also be thought of as a network? Over the last 10-15 years, and in opposition to latent variable interpretations of psychological constructs, a dynamical systems account of psychology based on networks has been formulated [110, 33, 34, 35, 36]. The network approach suggests that the behavioural, emotional and cognitive variables within individuals comprise a dynamic, self-organising web of interacting components. Specifically, each variable can be represented by a vertex or node, and edges connecting nodes represent real causal relationships (Figure 3). By ‘causal’, 485 the network approach posits that the occurrence of one variable (e.g. feeling sad)

can directly lead to the increased chance of another variable (e.g. sleeping less), conditional upon all other variables in the network. The network approach therefore rests on principles of causality based on conditional independence relationships on directed acyclic graphs instantiated by Pearl [141].

Functionally similar network components are predicted to hold stronger causal relationships, forming clusters of recurring components through space and time within individuals. Clinically depressed individuals, for instance, might show consistent feedbacks between symptoms, such as ‘fatigue’ → ‘concentration problems’ → ‘low mood’ [142]. Depression is not some latent variable to ‘have’ or ‘not have’, therefore, but may be an emergent property of habitually expressed symptoms through time and space [142, 143], in the same way that collective animal behaviours are emergent properties of relatively simple rules between individuals or functional brain networks are emergent properties of synaptic activity [117]. Cross-correlations between constructs, such as comorbidities between generalised anxiety and depression, which complicate assumptions of unidimensionality in reflective latent variable models (i.e. manifest variables should only load on one factor), are naturally handled in the network view as it does not constrain correlations between diverse components and recognises the fuzzy boundaries between many traits [34, 144]. Networks are additionally equipped to handle problems of degeneracy and redundancy [117, 118] because different components may contribute to the same component-clusters, and the same component can contribute to different clusters.

The measurement relationship in this instance is neither operational, formative nor reflective, but *mereological*: “the observables do not measure the construct, but are part of it” [145, p. 47] (see also Borsboom & Cramer [146] or Borsboom *et al.* [36]). This is not operationalism disguised: computing a network of relationships between variables is not enough to evidence the network approach, and in fact network models can be shown to be statistically equivalent to some latent variable models [147, 148]. Instead, the network approach asserts that causal relationships exist between behaviours through time and space, and it is the nature of these causal processes (e.g. exciting or inhibiting) that define the organisation of behaviour. This causal behavioural system exists *independently* of the operations used to characterise it. Borrowing from Boyd’s [149] defense of viewing natural kinds (e.g. species) as ‘homeostatic property clusters’, Kendler [150, p. 1147] argued that psychiatric disorders were best understood as mechanistic property clusters: the properties (symptoms) “are not similar merely in their superficial properties...but because the co-occurrence of these properties from individual to individual is explained by causal mechanisms that regularly ensure these properties are instantiated together”. The causal mechanisms dictating behaviour may indeed include genetic, neurobiological or physiological variables as part of the causal behavioural system. However, these variables also exist in their own right and are not relegated to latent variables.

The network approach has burgeoned into a highly active discipline with widespread theoretical [151], fundamental [36, 152], and clinical [153, 144] significance to human

psychology. Network models are employed using causal modelling techniques such as the Gaussian graphical model for metric variables, the Ising model for binary variables, and multivariate vector autoregressive models for time-varying data [151]. Network models have, furthermore, been applied in a hierarchical structure [154], which demonstrated inter-individual variation in network structures (e.g. the sign and magnitude of partial correlations between behaviours). In terms of the requirements for a suitable measurement model for animal personality, networks models account for the theoretical construct and observed variables (the construct is an emergent property of the network), apply to individuals and not to aggregates, are causal hypotheses of behaviour, can be applied to time- or context-varying data, and also allow one arbitrary flexibility to include additional variables that influence behavioural variables. For example, Isvoranu *et al.* [155] include environmental risk factors into their network model of psychosis, such as developmental trauma. Although network models have faced their own criticisms [148, 147, 156], they have received widespread support from across human psychology, with researchers actively working on network theory, methodology and replicability [151, 157].

Few studies have considered the network approach to understand behavioural phenotypes in animals. Wilkins *et al.* [158] presented a network approach to understand multi-modal communication signalling in American barn swallows (*Hirundo rustica erythrogaster*), and others have encouraged a systems approach to animal communication [159]. Goold *et al.* [37] used network analysis to understand cross-sectional owner reports of working dog behaviour, including the use of network centrality measures and estimation of network robustness. More recently, Martin *et al.* [38] motivated a combined exploratory graph analysis—generalised network approach [151] that combined factor analysis with network models of residual pairwise correlations to investigate behavioural syndrome structure in common marmosets (*Callithrix jacchus*). The latter authors provide a cohesive overview of the utilities of network modelling in addition to latent variable modelling on statistical and empirical grounds.

Given the growing support for network models in human psychology, as well as across scientific areas, the network approach may offer a unifying measurement model to understand animal personality, behavioural syndromes, and individual variation. Hierarchical network models [154] would allow the continued estimation of individual-varying parameters to conduct variance components analyses and calculate behavioural repeatability. Correlations between behaviours, such as behavioural syndromes, are naturally represented because the core of network approaches is estimating regularised networks of partial correlations between behaviours. Importantly, the theoretical concept of state-behaviour feedback loops [130] should find immediate application in network models by including state variables directly as network variables. Lastly, network models are not completely opposed to latent variables, meaning latent variables may also be included where appropriate or practically useful (e.g. Martin *et al.* see [38]). While a lot of work remains to be done to formulate a network measurement model for animal personality, there is a pressing need for a uni-

fyling measurement framework in animal personality, and network models represent the current state-of-the-art.

5 Conclusion

I have reviewed measurement models in animal personality science, and demonstrated how debates that personality is anthropomorphic, too descriptive, and lacking theoretical rationale can be linked to a lack of unified approach to measurement. Interestingly, these problems parallel similar debates in human personality, which are important to heed. Network models provide a particularly intriguing form of measurement model that may be of substantial interest to animal personality scientists. Not only does the network approach accommodate existing concepts such as behavioural repeatability and behavioural syndromes, it integrates with theoretical models such as state-dependent models and offers a more explicit hypothesis for the generation of behaviour than operational or latent variable approaches.

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