

**Cross-Species Comparisons of Individual Differences in Social Behaviour:
Methodological Challenges and Solutions**

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Abstract

Cross-species comparisons of individual differences in social behaviour offer opportunities to address central questions in both biology and psychology. Behavioural ecology typically pursues such comparisons to understand how behavioural traits evolve across taxa, whereas personality psychology has largely focused on humans, with other species often serving as models for human behaviour. Although methodological advances have broadened the scope of such comparisons, establishing that behaviours are functionally equivalent across species remains a central challenge. In particular, anthropocentric constructs and assessments that ignore species-specific sensory and ecological demands have constrained progress. We argue that meaningful cross-species inferences about individual differences in social behaviour require explicit methodological alignment. Drawing on both disciplines, we propose locating behaviours according to their social function within established coordinate spaces such as the interpersonal circumplex. This allows functionally equivalent behaviours to be compared across taxa despite differences in their observable form. We illustrate this approach at two interconnected stages of research on individual differences: (i) conceptualisation, by defining and aligning behavioural constructs across taxa, and (ii) assessment, by developing functionally equivalent and ecologically relevant measures. Such alignment transforms cross-species comparison from descriptive analogy into rigorous inference about individual differences in social behaviour.

Keywords: animal personality, individuality, functional equivalence, interpersonal circumplex, behavioural assessment

Cross-Species Comparisons of Individual Differences in Social Behaviour: Methodological Challenges and Solutions

Individuals of the same species differ consistently from one another in their behaviour. Such individuality in behaviour is found in humans (e.g., Borkenau et al., 2004; Breil et al., 2023; Funder & Colvin, 1991) and in other animals (e.g., invertebrates: Niemelä et al., 2015; Santostefano et al., 2016; fish: Bell, 2005; Dingemanse et al., 2007; amphibians: Kelleher et al., 2017; Mühlenhaupt et al., 2026; Peignier et al., 2022; birds: David et al., 2012; Nicolaus et al., 2012; mammals: Herde & Eccard, 2013; Miguel et al., 2024), making it a fundamental feature of biological systems (Bell et al., 2009; Kaiser & Trappes, 2021). Understanding why such individual differences in behaviour emerge, how they are expressed and maintained, and what consequences they have is important for explaining processes ranging from the formation of social relationships and the organisation of social systems to species interactions and ecosystem processes (Wolf & Weissing, 2012). Comparing individual differences across species further places these questions in a broader evolutionary and ecological context by revealing which patterns are widespread and general, which are shared among species with similar ecological conditions or evolutionary histories, and which are species-specific. Comparative analyses are a classical approach in behavioural ecology to understanding how behaviour has evolved across species (Tinbergen, 1963). More recently, the focus has expanded to include comparisons of individual differences across species, an approach that is also increasingly informing personality psychology (Kuper et al., 2025; Laskowski et al., 2022; Nettle & Penke, 2010). Such comparisons remain constrained, however, by the challenge of establishing comparability across species (Uher, 2008a, 2008b).

In this paper, we take up this challenge for a particularly demanding case: individual differences in social behaviour. Social behaviour describes the behaviour of an individual that is

meaningfully related to other individuals through interaction, social situatedness and/or responsiveness, social directedness, or socially relevant consequences (Kaiser et al., 2026). Social behaviour is demanding to study because it is relational: Its expression depends on the interacting partners and the structure and dynamics of the social unit as much as on the individual itself (Back et al., 2011; Webster & Ward, 2011). Furthermore, comparing individual differences in social behaviour across species is especially difficult because the behaviours involved may differ markedly between species even when they have comparable consequences. Consider the following three examples. Some cooperatively breeding cichlids such as *Neolamprologus pulcher* (hereafter, cichlids) consistently chase and bite others, while others retreat (Reddon et al., 2019; Riebli et al., 2011), some voles scent-mark extensively over large areas in the presence of rivals while others withdraw and mark little (Erixon et al., 2024), and some humans overemphasise their own performance at others' expense in group interactions while others hold back (Härtel et al., 2023). These behaviours differ, but they have a similar consequence: securing precedence at others' expense.

Behavioural ecology and personality psychology have approached cross-species comparisons of individual differences from different starting points. In behavioural ecology, behaviour is observed directly and interpreted in relation to the ecological and social challenges an organism faces, which allows comparative predictions to be derived from evolutionary theory. Research on individual differences within this tradition has largely remained within single species or populations. Where comparisons occur, they are often across populations of the same species (e.g., *Apodemus agrarius*: Dammhahn et al., 2020; *Gasterosteus aculeatus*: Dingemanse et al., 2007; *Parus major*: Mouchet et al., 2021). Comparisons across species have often focused on specific behaviours or behavioural responses, frequently using a common assay (i.e., an identical assessment procedure) across closely related species or adapting a simple assay to

different species. Much of this work has concerned non-social behaviours such as exploration and neophobia, where a common stimulus can be presented across species (e.g., Carter & Feeney, 2012; Mettke-Hofmann et al., 2002; Miller et al., 2022; Schaffer et al., 2021; Sommer-Trembo et al., 2024). More recently, large collaborative efforts such as the ManyBirds project have extended this logic across a broader range of avian species by adapting equivalent novel-object tests to different species (Lambert et al., 2022; ManyBirds Project et al., 2025). These approaches provide important opportunities to examine phylogenetic and ecological patterns in individual variation. What is compared, however, is often operationally defined by the specific assessment procedure itself, making it difficult to establish whether the measured behaviours are genuinely equivalent across species.

Personality psychology has proceeded differently. Research on individual differences rarely targets a single behaviour. The variable of interest is usually an aggregate, most often across a set of questionnaire items answered by the participants themselves (Paulhus & Vazire, 2007). Where behaviour itself is observed, multiple indicators are typically assessed across a variety of situations (Borkenau et al., 2004; Breil et al., 2023; Funder & Colvin, 1991). Aggregation of this kind yields more reliable and more generalisable variables than single behaviours (Epstein, 1979). Such variables are placed within well-established taxonomies of individual differences (Ashton & Lee, 2007; Goldberg, 1990; John & Srivastava, 1999). When extended to other species, however, psychological work has largely proceeded from an anthropocentric perspective. This is reflected both in the methods, with trait constructs and rating instruments developed for humans being applied to other species (e.g., Gosling & John, 1999; King & Figueredo, 1997), and in the interpretation of results, which often focuses on understanding humans (e.g., Gosling, 2001; Mehta & Gosling, 2008). While studies suggest that aspects of human trait structure can be recovered in many of the species investigated, much of

this research has concentrated on primates (e.g., Freeman & Gosling, 2010; Koski, 2011b; Uher & Asendorpf, 2008; Weiss et al., 2007), pets (e.g., Gosling et al., 2003; Zeigler-Hill & Highfill, 2010), or farm animals (e.g., Finkemeier et al., 2018). Such research has also been criticised because the recovered structure rests on trait adjectives whose meaning is supplied by the rater rather than anchored in the observed behaviour (Uher & Visalberghi, 2016).

Thus, each tradition brings its own strengths and offers complementary tools for comparative research. Behavioural ecology brings experience with a broad range of species, the evolutionary and ecological background against which behaviour is interpreted, and methods for evoking and assessing specific behaviours in defined ecological or social contexts. Psychology brings variables that remain interpretable across situations, psychometric approaches for measuring individual differences, and trait taxonomies in which such variables can be placed. In line with previous work, we argue that comparisons of individual differences in social behaviour across species can benefit from integrating both traditions (see also Carter et al., 2013; Delval et al., 2024; Gosling, 2001; Koski, 2011a; Kuper et al., 2025; Nettle & Penke, 2010; Weiss, 2018). Such an integration rests on a basic requirement. Individual differences must be rooted in the behavioural repertoire of each species and not inferred from abstract trait labels. These behaviours then have to be related to one another at a level of organisation at which species can be compared (see also Uher, 2008a, 2008b). We propose that this level is the social function a behaviour serves. Functionally equivalent behaviours can then be organised within a common framework that locates different social functions relative to one another.

Meaningful cross-species comparisons of individual differences in social behaviour therefore require methodological alignment instead of assumed comparability between superficially similar social behaviours or behavioural measures. To achieve such alignment, we focus on two stages of research: (i) the conceptualisation of individual differences in social

behaviour, that is, defining and aligning behavioural constructs across taxa, and (ii) their assessment, that is, designing ecologically relevant and functionally equivalent measures.

Throughout, we use the interpersonal circumplex (Leary, 1957; Wiggins, 1979) as an example of a common framework in which social functions can be located. Our aim is to demonstrate how cross-species comparisons can be methodologically grounded during the planning of new studies and in the evaluation of existing ones.

Conceptualisation of Individual Differences in Social Behaviour

Within-species studies often focus on single behaviours or behaviours measured within a single assessment procedure, without establishing their relation to a broader trait. For many within-species questions this can be sufficient. Whether individual cichlid fish consistently differ in how often they chase and displace other fish can be established, and these differences can be related to other variables, without deciding which broader trait category chasing and displacing belong to. In practice, researchers in the field of behavioural ecology often refer to such behaviours using broader trait labels, without the multi-indicator assessment and validation procedures typically used to establish traits in psychology (for human behavioural examples that use a multi-indicator assessment, see Breil et al., 2023; Funder & Colvin, 1991; Leising & Bleidorn, 2011). However, avoiding broad, unvalidated trait labels in favour of describing specific behaviours has been explicitly recommended (Beekman & Jordan, 2017; Dingemanse & Wright, 2020; Roche et al., 2016).

While within-species studies can examine consistent individual differences in specific behaviours without establishing a link to a broader trait, cross-species comparisons require individual differences to be defined at a level that extends beyond species-specific behaviours or assessment procedures. This level cannot be that of behaviour itself, because (i) behaviours that differ in how they appear may perform a similar role (e.g., chasing and displacing in cichlid fish,

scent-marking by voles, and overemphasising one's own performance at others' expense in humans), and (ii) behaviours that look alike may perform different roles. For example, in closely related poeciliid fishes, tail beating has been described as an agonistic behaviour in *Brachyrhaphis olomina* (Garita-Alvarado et al., 2018), whereas a similar movement, termed "tail slapping", was interpreted as an avoidance response in *Xiphophorus* species (E. Clark et al., 1954). Comparability must therefore be established at the level at which the behaviour works. This level is the function the behaviour serves.

This emphasis on function is not new. Behavioural ecology has long been concerned with determining the function of behaviours in terms of their value for survival and reproduction (Tinbergen, 1963). Function has also been proposed as a basis for establishing comparability across species. For example, Uher (2008b) called for basic principles to establish the functional equivalence of non-identical behavioural indicators and situational properties across species. Function can be understood in different ways, and different theoretical accounts can be distinguished, including selected-effect functions and causal-role functions. Selected-effect functions (e.g., Neander, 1991; Wright, 1973) are the effects for which a behaviour was selected and thus determined by evolutionary history. This view aligns directly with ultimate explanations of adaptive significance. In contrast, causal-role functions (e.g., Amundson & Lauder, 1994; Cummins, 1975) characterise the role a behaviour plays within the larger system in which it occurs. Rather than tracing historical selective origins, causal-role analysis provides a systemic account of how a behavioural interaction operates in the present. For example, tail quivering in cichlids can function as a signal of appeasement. The behaviour occurs when a smaller individual is attacked by a larger conspecific and, instead of fleeing, remains in a vulnerable position while quivering its tail. The behaviour is followed by a reduction in subsequent attacks by the dominant, suggesting that its causal role is to appease the dominant and reduce further

aggression (see Ruberto et al., 2024; Taborsky & Grantner, 1998). This present causal role may not be the one that tail quivering was selected for historically. That is, it could have originated for a different social effect such as general affiliative signalling.

For the purpose of meaningful cross-species comparisons of individual differences in social behaviour, we focus on function in the causal-role sense. Because individual differences in social behaviour take effect within a social unit, we take the system to be the social unit in which a behaviour occurs and ask what role it plays there. We refer to this role as the *social function of the behaviour*. The role a behaviour plays within the social unit is identified by its consequences, that is, the change it typically brings about in the social situation. In the cichlid example above, the reduction in subsequent attacks is such a change. A change of this kind may be a response directed at the acting individual or a shift in the social situation itself, such as gaining access to a contested resource. It depends on how others respond, and it need not follow immediately, as when another vole encounters a scent mark deposited earlier.

A behaviour's typical consequence depends on the situation (i.e., short-term, temporally and spatially bounded circumstances that are external to an individual; Kuper et al., 2026; Rauthmann et al., 2015) in which the behaviour occurs. In three-spined sticklebacks, for example, behaviours such as biting and charging occur both in territory defence and during courtship interactions, yet with different consequences in each case (Le Comber et al., 2003; Rowland, 1988). Function is therefore ascribed to a behaviour in a particular situation type, not to a behaviour as such. Within a situation type, function refers to the typical consequence of a behaviour, that is, the consequence a behaviour *usually* has, even if other consequences occur in individual instances. For example, tail quivering by a subordinate cichlid fish under attack from a dominant may occasionally not result in appeasement (e.g., because the dominant continues or

escalates the attack, which can lead to eviction from the group), but this does not alter its typical consequence of appeasement.

Determining the function of a behaviour within a species is thus an empirical step, and this process proceeds in two stages. First, knowledge of the natural history of the species is needed to identify the behaviours in its repertoire and the situations in which they typically occur (see also Uher, 2008a, 2008b). Second, the behaviour is characterised functionally by what typically follows it across individuals and occasions within a given situation type. The resulting functional characterisation is based on the behaviour's consequences rather than on the label a human observer would intuitively assign to it. In establishing social functions, two related questions are deliberately set aside. We do not ask how such roles came about, nor what they contribute to survival and reproduction. Both are questions for research, and both are among the things that cross-species comparisons can address. They therefore cannot define the constructs being compared. Chasing a rival, for example, may typically cause the rival to withdraw, and it may or may not also contribute to survival or reproductive success over an individual's lifetime. Only the first counts as a social function in our sense.

Although the behavioural expressions and repertoires remain species-specific, social functions as described above recur across species. These functions can be understood in relation to common challenges of social life. Individuals living among conspecifics, for example, commonly face two problems: securing precedence (e.g., Drews, 1993; Strauss et al., 2022; Tibbetts et al., 2022) and maintaining cooperative bonds (Clutton-Brock, 2009; de Waal, 1986; Silk, 2007). These two problems correspond to two separable components of the consequences of a social interaction. The first is the allocation of precedence and access to contested resources between the interacting individuals, that is, which of them prevails. The second is how cooperative bonds and tolerance are affected, that is, whether the interaction strengthens or

weakens them. Neither follows from the other and both can be assessed independently, since precedence can be secured or ceded whether the bond is strengthened or weakened. Both can be determined from the observable course of the interaction. Personality psychology has arrived at the same two components and refers to them as “getting ahead” (securing precedence) and “getting along” (maintaining bonds; Hogan & Blicke, 2018; Hogan et al., 1985). We adopt these labels because they offer a parsimonious basis for sorting social functions. Because the two components can vary independently, they can be treated as two axes, and a social function can be located along both axes by asking how the behaviour allocates precedence and how it affects cooperative bonds.

To illustrate how this placement works, we return to three behaviours in three different species, each observed in a situation in which a rival is present and priority between the two is at stake. A cichlid fish repeatedly bites and chases a rival away from a contested shelter, and the other gives way (Reddon et al., 2019; Riebli et al., 2011). A vole marks a contested area heavily with urine, and the rival withdraws and marks little in return (Erixon et al., 2024). In a discussion, a person overemphasises their own performance and dismisses another’s contribution (Härtel et al., 2023), and the other stops pressing the point. In appearance, the three behaviours share almost nothing. The first is a direct physical displacement, the second a chemical signal spread across space, and the third a verbal exchange. What they share are functionally corresponding situations and similar consequences that typically follow within each species. In each case, the rival gives way and the actor gains priority of access to the contested resource (e.g., the shelter, the space, the credit for the contribution), which is a getting ahead consequence. At the same time, these behaviours are likely to reduce tolerance or strain the relationship between the individuals, suggesting a low position on the getting along axis. On these grounds, the three behaviours fall in the same region, high on the getting ahead axis and low on the getting

along axis. They are placed together not because they resemble one another but because they occur in functionally corresponding situations and their typical consequences are similar along both functional dimensions.

Once functions are placed on these two axes, they fall into a shared space that corresponds to the interpersonal circumplex (Leary, 1957; Wiggins, 1979; see also Bakan, 1966; Dawood et al., 2018; Gurtman, 2009; Hopwood et al., 2021; Wiggins & Broughton, 1991). Positions in this space are combinations of getting ahead and getting along, and four bipolar axes run through it. Two are getting ahead and getting along themselves, and the other two are mixtures of both. The poles of these four axes define eight distinguishable positions, each of which carries an established label (see Figure 1). The position the three behaviours described above share is the one labelled *competitive*. Each position can accommodate a range of behaviours within a given species, and the same position can be occupied by very different behaviours in different species (see Table 1 for examples).

Figure 1

The Interpersonal Circumplex

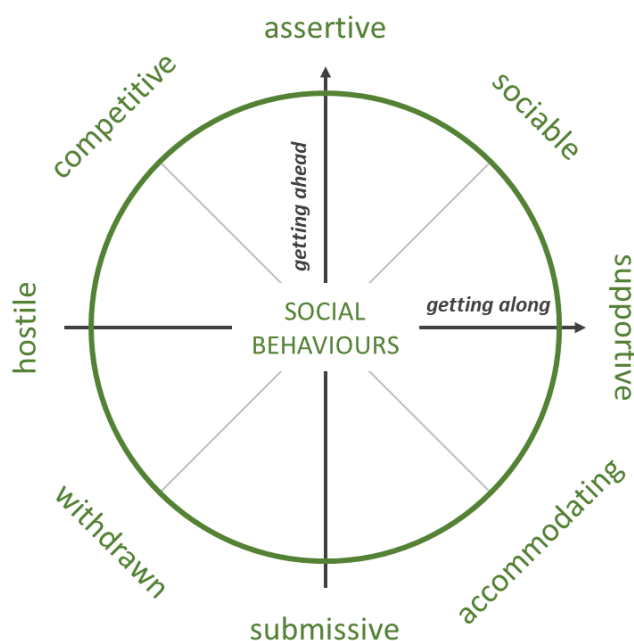


Table 1*Illustrative Placement of Species-Specific Behaviours Along the Two Functional Dimensions*

Social Function	Label	Human	Cichlid	Vole
Secures precedence at the other's expense and weakens cooperative bonds (getting ahead high, getting along low)	competitive	In a group discussion, dismisses another's contribution and promotes their own	At a contested shelter, performs threat displays, bites and chases another fish away	With a rival present, marks the contested area extensively
Secures precedence without strengthening or weakening cooperative bonds (getting ahead high, getting along neutral)	assertive	At the start of an unstructured task, sets out the steps and assigns them	Occupies a breeding shelter without biting or chasing	With no rival present, marks along its range boundaries
Secures precedence and strengthens cooperative bonds (getting ahead high, getting along high)	sociable	In a group task, proposes how to proceed and asks quieter members for their views	Enters a shelter occupied by a smaller group member and settles in it while the smaller fish also stays in it	In a shared range, continues to use the core area and forages near a neighbour without attacking
Strengthens cooperative bonds without allocating precedence (getting ahead neutral, getting along high)	supportive	In a casual conversation, lets the other finish and endorses their point	Digs sand out of the shelter of group members and carries it away	Outside the breeding season, nests communally with a small group
Cedes precedence and strengthens cooperative bonds (getting ahead low, getting along high)	accommodating	In a disagreement, yields the floor and supports the other's proposal	When bitten by a larger group member, stays in place, quivers its tail, and remains next to it	In the overlap zone, moves aside for a familiar neighbour and continues foraging next to it
Cedes precedence without strengthening or weakening cooperative bonds (getting ahead low, getting along neutral)	submissive	When another person states a decision, goes along with it without contesting or adding anything	When a larger fish approaches the shelter it occupies, leaves the shelter and finds another shelter	When a resident approaches, moves off in the opposite direction without displays or contact
Cedes precedence and weakens cooperative bonds (getting ahead low, getting along low)	withdrawn	In a group task, stays silent and turns away from the group	In a group, occupies a position at the territory border and stays apart	When conspecifics are active nearby, retreats into the burrow
Weakens cooperative bonds without allocating precedence (getting ahead neutral, getting along low)	hostile	When approached in a friendly manner, responds with a dismissive remark	Bites and chases a group member across the territory border and then returns to its own position	Away from the nest, chases and bites a conspecific that approaches

Note. The table illustrates how behaviours, their social functions, and descriptive labels relate to one another. The behaviours shown are plausible instances of behavioural repertoires described in the literature (Humans: Funder et al., 2000; Grünberg et al., 2018; Härtel et al., 2023; Cichlids: Fischer et al., 2017; Hamilton et al., 2005; Jordan et al., 2021; Reddon et al., 2019; Reyes-Contreras et al., 2019; Voles: Dobby, 2005; Erixon et al., 2024; Gromov, 2023; Heise & Rozenfeld, 2002; Power et al., 2025). Their assignment to social functions is illustrative and not established. Confirming it would require validating each behaviour's typical consequences within a given situation type.

Using these labels allows behaviours to be related across research traditions that describe them in different vocabularies, and organising social behaviour in this way has been proposed for other species and across disciplines before (Kuper et al., 2025; Zeigler-Hill & Highfill, 2010, 2017). These and related labels are used differently across traditions and sometimes within them. For example, dominance refers to a behavioural tendency in personality psychology (e.g., Fournier et al., 2008; Leikas et al., 2012), whereas in much of behavioural ecology it refers to social rank, often understood as the outcome of previous contests (Tibbetts et al., 2022). Sociability is used in both traditions for a tendency to approach and associate with conspecifics (Réale et al., 2007; Soto & John, 2017), which does not always involve an allocation of precedence and therefore does not necessarily coincide with the position labelled sociable in the circumplex. We do not propose to settle these usages. Placement follows from the social function, that is, from the typical consequence within a given situation type, and the label only names the resulting position. We also do not claim that the two axes are exhaustive. Further or more fine-grained functions can be added wherever they can be established within species in the same way. Using this space leaves open whether behaviour is organised in the same way across all species. However, it provides a common backbone for cross-species research questions and predictions, and it allows comparable hypotheses to be formulated even when social behaviours are expressed differently across species.

Functional equivalence is a necessary but not a sufficient basis for comparison. Locating a behaviour within a common functional framework establishes the dimension along which behaviours are compared, but not the property of individual differences under investigation, such as an average level, a response to a social or ecological gradient, or consistency across repeated measurements. Both the property under investigation and the level of aggregation must be

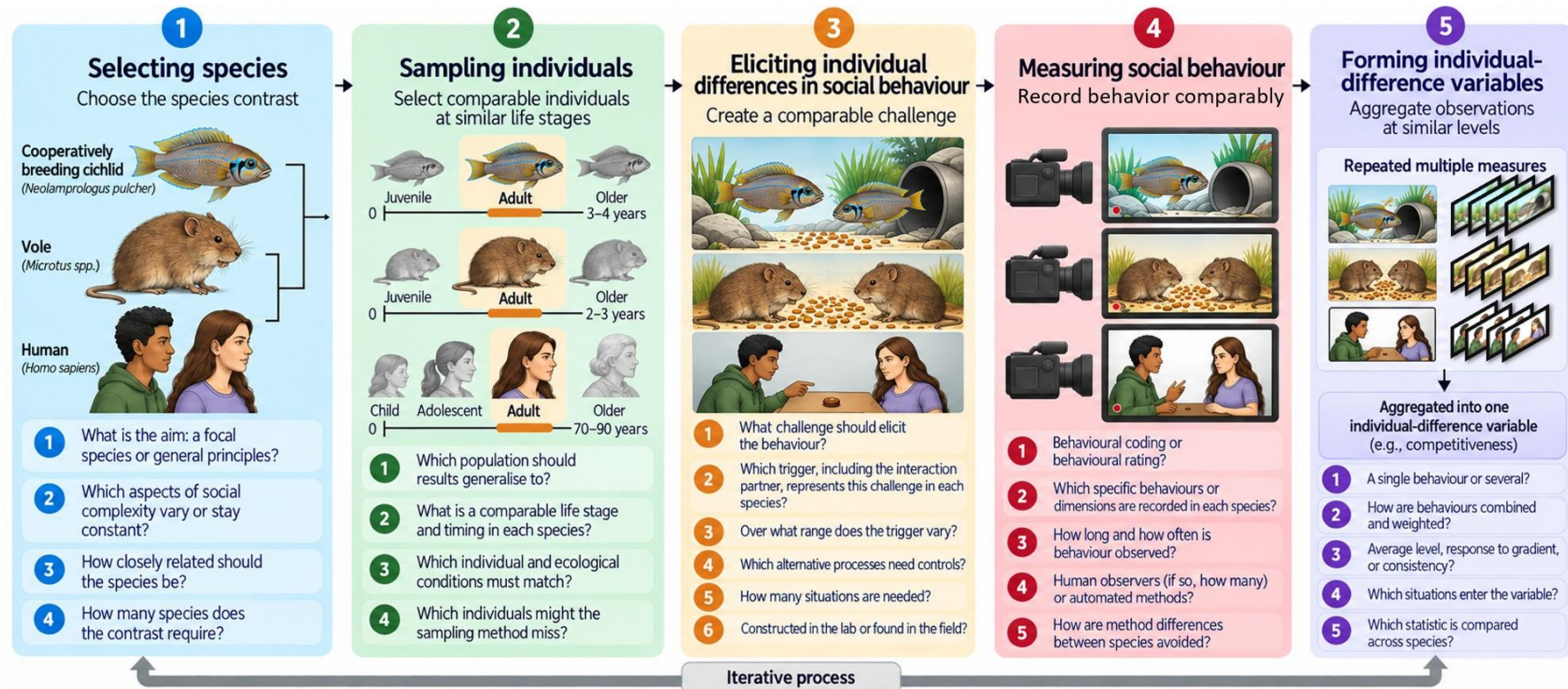
matched across species. How these specifications are realised in a given study is a question of assessment.

Assessment of Individual Differences in Social Behaviour

Assessment covers the decisions that turn a functionally defined construct into a measurable variable and follows different traditions across behavioural ecology and psychology. The fundamental challenge of cross-species assessment is that observed cross-species differences in individual variation can arise from two possible sources: They may reflect species differences in the expression of the behaviour, or they may be produced by the assessment itself (Uher, 2008a, 2008b; van de Vijver & Tanzer, 2004). This ambiguity arises at every point in the measurement process, even when the behaviour has been functionally conceptualised: whether individuals are sampled at comparable life stages and under comparable conditions relative to each species, whether assessment procedures create comparable functional challenges (situational triggers), whether observation tools register comparable aspects of behaviour, and whether raw observations are converted into comparable variables. Each of these steps requires a separate judgement about equivalence. Thus, cross-species comparisons require alignment across the entire measurement pipeline, from sampling to the formation of variables. These decisions are typically preceded by the choice of species itself (see Figure 2 for an overview of all steps and decisions).

Figure 2

A Decision Framework for Designing Comparable Assessments of Individual Differences in Social Behaviour Across Species



Note. Five linked stages guide species selection, individual sampling, eliciting social behaviour through comparable challenges, social behaviour measurement, and construction of comparable individual-difference variables. Each stage lists guiding questions. The process is iterative, allowing decisions at later stages to inform earlier ones. Images were produced using generative AI (ChatGPT, OpenAI).

Selecting Species

Species should be selected on theoretical grounds. The relevant species are therefore not necessarily those that are most closely related, those that show similar-looking behaviours, or those that are easiest to sample. Which species to compare depends on the aim, whether that is learning about a focal species such as humans or tracing individual differences to shared ancestry, ecology, or broader adaptive principles. A key dimension is social complexity, considered in terms of specific characteristics of the social organisation, social structure, mating system, and care system (Kappeler, 2019). Depending on the question, these characteristics can be varied systematically across species or held constant to isolate other factors. The same logic applies to phylogenetic relatedness: Closely related species may provide a particularly strong test when they are sufficiently similar in relevant aspects to isolate the factor of interest, whereas distantly related species allow general adaptive principles to be examined when they provide comparable functional indicators. For each species, it must be established that the target behaviour can be reliably identified and functionally characterised, and that the species can be sampled representatively. Because species are not independent observations, phylogenetic covariance has to be accounted for when patterns across species are interpreted (Felsenstein, 1985), and the number of species required should be determined by the contrast being tested.

Sampling Individuals

Sampling is the first point at which differences between species can be produced by assessment decisions. The goal is to obtain, for each species, a sample that is representative of the population one aims to generalise to, with respect to the characteristics that are relevant for the behaviour under study. What this requires depends on how broad or specific that generalisation goal is. For example, individual differences in competitive behaviours may change with age as individuals acquire different social experiences. Thus, a sample containing only

adults may capture a different pattern of individual variation than one that includes juveniles as well, limiting generalisation across life stages. Which individuals belong in the sample therefore depends on the claim being made.

Across species, the samples then also have to be comparable to one another:

Comparability in sampling is relative, and each sample should represent a comparable part of the range of variation within its respective species. Individuals should be sampled at comparable developmental or life stages and, where behaviour varies across the day or seasonally, at comparable points in the daily or annual cycle (e.g., Chmura et al., 2020; Day et al., 2009). Repeated measurements should also be spaced relative to the species' lifespan so that they capture comparable temporal stability (Dingemanse & Wright, 2020). Relevant individual characteristics such as sex, health, experience, including rearing and housing conditions, and social status should also be aligned or accounted for where they systematically influence behaviour (see also Webster & Rutz, 2020). Where individuals are sampled from the field, the populations they come from should likewise be at comparable points in terms of density, resource availability, predation risk, and abiotic conditions such as temperature. Of course, full alignment is often unrealistic in practice, and remaining differences should then be documented. Selection bias presents an additional concern, particularly in field studies: Individuals that are easier to capture, observe, or habituate may systematically differ in behaviour from those that are not (Biro & Dingemanse, 2009). Together, these decisions help ensure that observed differences between species reflect the individual differences of interest rather than differences in when, where, or in whom the behaviour was measured.

Eliciting Individual Differences in Social Behaviour

Once species have been selected and the relevant individuals have been identified, researchers must decide how to create or choose assessment situations that elicit individual

differences in the behaviour of interest. Individual differences are typically elicited not by a situation as a whole but by particular aspects of it. We refer to such an aspect as a situational trigger, that is, a specific aspect of the environment that is present in a bounded instance in time and space and evokes different behaviours in different individuals (see Breil et al., 2022; Kuper et al., 2026; Rauthmann et al., 2015; see also the principle of trait activation: Tett & Guterman, 2000). Cross-species assessment requires situational triggers that may differ between species but pose the same functional challenge, eliciting behaviours that serve as indicators of the same functionally defined construct.

In practice, comparative research has often applied the same standardised task across species for numerical comparison, which may obscure important differences in what the task represents to each species and constrain the kinds of research questions that can be answered (see also Carter et al., 2013; Martin et al., 2023). For example, responses to a mirror test in fish can be interpreted as aggression or as sociability depending on the species (Cattelan et al., 2017; Josi & Frommen, 2021), indicating functionally different behaviours. Likewise, the open field test, in which individuals are removed from their “home environment” and placed in a barren, enclosed arena, was developed for rodents, which experience open areas as risky, whereas birds navigate space differently because of flight and broader visual fields. Avian versions therefore require substantial modification, and apparently similar tests may not measure equivalent processes (Perals et al., 2017). Assessment procedures should instead incorporate and validate the situational triggers that elicit individual differences in functionally equivalent behaviours in each species. Comparative cognition has already moved in this direction, with species-specific paradigms designed to target the same process and validated separately in each species (e.g., Kabadayi et al., 2018; Massen et al., 2019; Schubiger et al., 2020). Similarly, a proposal for assessing cooperation holds the ranking of outcomes and the repetition of interaction with an

identifiable partner constant while adapting the response device, the reward, and the sensory channel to each species (Siestrup et al., 2026).

When designing such a procedure, the aim is to make individual differences in the target behaviour as pronounced and stable as possible. This requires a series of linked decisions about how assessment situations are created and sampled. The position of the target behaviour's social function within the interpersonal circumplex (see Figure 1 above) can guide these decisions, because it specifies the type of social challenge the situation must present in order to elicit individual differences in functionally equivalent behaviours across species. First, researchers need to specify the social or ecological challenge expected to generate individual differences in the target behaviour. To evoke individual differences in competitive behaviours, this calls for a situation in which one individual can secure a resource at the expense of another. A situation that produces the same response in every individual acts as a situational constraint rather than a trigger (Meyer et al., 2010), as when a resource is so abundant that no contest arises, for example, when food is distributed widely enough for every fish in a shoal to feed undisturbed. Second, they need to identify the species-specific triggers that best represent this challenge while remaining functionally equivalent across taxa. In cichlids, this may be a single shelter that only one individual can occupy at a time, in voles a restricted food source or a contested passage at a shared range boundary, and in humans a task with a single reward that an unfamiliar individual also claims. Third, they need to determine the range or gradient of the trigger that will be presented and how it is measured, such as the number of rivals at the resource, the size asymmetry between the focal individual and its opponent, or the value of the reward at stake. Fourth, they need to identify alternative processes that could generate the same behavioural response, such as fear or general stress in a situation intended to evoke competitive behaviour, and design controls or complementary situations where necessary. Finally, they need to

determine how many situations are required to establish that the resulting individual differences generalise beyond a single situation.

The choice of trigger is particularly demanding for social behaviour, where the trigger is often the interaction partner, whose responses in turn make the level of the gradient harder to hold constant (Hopwood et al., 2020). In humans, partners can be instructed, so that a confederate behaves dominantly or warmly while other aspects of their behaviour are kept constant (Breil et al., 2022; Leikas et al., 2012; Oliver et al., 2016). In other species, the corresponding levels can be established by selecting partners with known attributes, such as a larger or smaller opponent, a familiar neighbour or an unfamiliar intruder, or a conspecific of known aggressiveness (e.g., Erixon et al., 2024). Where the attribute is itself a behavioural tendency, as with a conspecific of known aggressiveness, it has to be established through pre-assessments. Non-responsive stimuli such as mirrors, models, or playbacks offer greater control over the social partner, but at the cost of the reciprocity that characterises natural social behaviour. Advances in robotics and virtual reality are beginning to address this limitation (Landgraf et al., 2021; Witte et al., 2017). Whether such stimuli work at all depends on the sensory channel they use. The context of the presentation is equally important. Outside the dispersal season, a call that would otherwise attract conspecifics may simply be perceived without posing the intended functional challenge. Table 2 gives examples of triggers for four social functions, showing how the same functional challenge can be presented differently across species.

Table 2

Illustrative Examples of Functional Challenges and Corresponding Situational Triggers Across Species

Label and position	Functional challenge posed	Human	Cichlid	Vole
Competitive <i>getting ahead high, getting along low</i>	Opportunity to monopolise a resource at a rival's expense	Task with a single reward and an unfamiliar partner instructed to claim it	Single shelter with an unfamiliar, size- and sex-matched rival present	Restricted food source with an unfamiliar, size- and sex-matched rival present
Assertive <i>getting ahead high, getting along neutral</i>	Opportunity to take precedence over a contested outcome in a situation that does not threaten the relationship	Two-person task requiring a decision and equal stakes with no assigned leader	Unsettled priority of access to a preferred shelter with a familiar conspecific present	Unsettled priority of access to a preferred nest site with a familiar conspecific present
Sociable <i>getting ahead high, getting along high</i>	Opportunity to engage with conspecifics while taking precedence	Two-person task with a shared goal, in which either partner can initiate and set the course of action	Group of conspecifics sharing resources that the individual can join	Occupation of a shared nest site by familiar conspecifics, which the individual can initiate and influence
Supportive <i>getting ahead neutral, getting along high</i>	Opportunity for conspecific cooperation or support	Task in which a partner is visibly struggling and can be helped	An egg predator that poses no threat to the individual itself approaches the brood while other group members are present	Shared nest with a familiar conspecific following temporary separation

Note. The table illustrates how the same functional challenge can be posed through different situational triggers across species. The triggers shown are examples of how each challenge could be implemented but may also elicit individual differences in behaviours at other positions of the circumplex.

These decisions apply whether assessment is conducted through standardised laboratory tasks or repeated observations in naturalistic settings. In laboratory studies, they guide the design and species-specific adaptation of experimental contexts. In field studies, they guide the selection of naturally occurring situations, the conditions under which observations are sampled, and the temporal and social range over which behaviour is assessed. What is standardised across species

is therefore the logic by which assessments are selected and justified, rather than the assessment procedure itself. For example, when assessing competitive behaviour over a monopolisable resource, the laboratory trigger is constructed. In humans, this can be a single reward and a partner instructed to claim it. The gradient varies with the number of rivals and the value of the reward, both of which are set by the design. In the field, the trigger has to be found where it naturally occurs, for example, on occasions when a scarce opportunity is allocated. The same gradient then has to be measured. A further difference is that the laboratory controls exposure to the situation, which sharpens the comparison because exposure to the trigger no longer varies between individuals, but also narrows it, since whether an individual enters such a situation at all is itself a relevant difference. Behavioural consistency in standardised laboratory conditions tends to be lower than in the wild (Bell et al., 2009), and there is a trade-off between standardisation of confounding factors and ecological realism to which monitoring in the field, remote tracking, and mesocosm experiments offer promising approaches (Gartland et al., 2022; Nathan et al., 2022). Where ecological or adaptive claims are made, laboratory conditions should therefore fall within the range the species normally encounters. Comparisons that draw on laboratory data for one species and field data for another are sometimes unavoidable. Functional equivalence of the triggers is then particularly important.

Measuring Social Behaviour

Social behaviour and the traits derived from it are typically measured in one of three ways. The first is direct observation, either in the situation itself or afterwards via video recordings (Bateson & Martin, 2021; Furr, 2009; Thorson & West, 2024). It can take two forms. In behavioural coding, observable actions or interaction patterns are quantified directly, often based on standardised ethograms (e.g., Koski, 2011b). In behavioural rating, a trained observer scores the observed behaviour on defined dimensions (Funder et al., 2000). The second is a

report by an informant who knows the individual (e.g., a researcher, a caretaker or, in humans, a friend or family member) and who integrates impressions across time and situations into a judgement on broader trait dimensions (Connelly & Ones, 2010; Gosling & Vazire, 2002). This approach has been especially influential in comparative primate personality research, where it has identified personality structures broadly resembling dimensions observed in humans (Gosling & John, 1999; King & Figueredo, 1997; Weiss, 2017). The third is self-report, which is the dominant approach in human research and is generally not available for non-human species (Paulhus & Vazire, 2007).

Only the first of these approaches captures actual behaviour (Back & Egloff, 2009; Kuper et al., in press) and supports comparison in the sense developed here. Informant reports and self-reports do not specify which behaviours in which situation types they draw on, so the assessment procedure is no longer clearly defined and the functional alignment established during conceptualisation can no longer be ensured. In addition, both are open to systematic distortion (Vazire, 2010). Informants bring their own expectations to the judgement (Uher & Visalberghi, 2016; Wessels et al., 2020), and different informants see the individual in different situations and therefore have access to different behaviours (Brandt et al., 2021). Self-reports are shaped by what individuals believe about themselves and by how they wish to appear (Paulhus & Vazire, 2007), and both rely on memory for past behaviour (Gosling et al., 1998). Informant reports and self-reports therefore converge only partly with observed behaviour of the same individuals (Kuper et al., in press; Šlipogor et al., 2020). For human research, this has direct consequences, since most assessments of individual differences in social behaviour rest on self-reports, and a comparison between a questionnaire-based self-concept and a coded interaction is not a comparison of behaviour. Experience sampling (i.e., repeated assessment of behaviour and other momentary states; e.g., Beal, 2015) captures behavioural self-reports closer to the moment, but it

remains a self-report with the limitations noted above. If psychology and human research are to take part in cross-species comparisons, observation of actual behaviour has to become standard practice on the human side, where it is still the exception (Baumeister et al., 2007; Furr, 2009; Kuper et al., in press). This can be complemented by ambulatory recording and mobile sensing, which capture aspects of social behaviour in daily life without relying on the individual's own account (Harari et al., 2020; Mehl & Pennebaker, 2003; Roos et al., 2023; Sun & Vazire, 2019).

The two forms of direct observation, coding and rating, are not necessarily comparable. While both can be equally valid, they may capture overlapping but non-identical constructs, because of the differences in the level of abstraction at which behavioural data are assessed (McGarrity et al., 2016; Morawska et al., 2015). Behavioural coding registers specific acts that then have to be aggregated upward to the functional category, whereas a rating is given directly at the level of the category or of the axis itself. The aggregation is therefore carried out according to explicit rules in one case and by the observer's judgement in the other, which makes ratings more vulnerable to human interpretation (see also Oostrom et al., 2019; Uher et al., 2013; Uher & Visalberghi, 2016) and coding more dependent on decisions about which behaviours and contexts are sampled. These differences become a problem when assessment traditions differ between the taxa compared, since a difference between species can then no longer be distinguished from a difference between methods. Whichever form is used, the behavioural categories or rating dimensions have to be formulated and tested separately for each species to ensure that they map onto the same functional category rather than onto behaviours that merely look alike. Likewise, sampling and recording rules, such as the length of observation periods, have to be set relative to each species' rate of behaviour. Assessments of the same behaviour also vary between observers. Behaviour should therefore be assessed by several trained coders or raters, so that idiosyncratic judgements average out.

Both coding and rating are also becoming considerably less costly. Recent advances in computer vision and machine learning substantially extend the possibilities for direct observation without constituting a separate form of measurement. Automated methods can identify individuals, track pose and movement, and quantify actions and interactions from large-scale video data (e.g., Fazzari et al., 2025; Zhong et al., 2026). They can therefore automate behavioural coding and increasingly derive higher-level behavioural representations from video or multimodal data. Their outputs nevertheless remain observation-based measures whose validity depends on how the extracted information maps onto the construct of interest. For cross-species comparisons, this adds a further source of non-equivalence: Model accuracy may differ across taxa because of morphology, visibility, recording conditions, or representation in training data, so that apparent species differences may partly reflect domain shift. Automated measures should therefore be validated across species and contexts, with model error treated as part of the assessment procedure.

Forming Individual-Difference Variables

The final assessment decision concerns how observations are aggregated and transformed into variables to study individual differences. The same set of behavioural observations can produce very different variables depending on which specific behaviours are included, how they are weighted, and whether observations are averaged across situations. Whether and how behaviours are aggregated within a situation depends on how broad the comparable construct is. When it refers to a relatively narrow aspect (e.g., the effort an individual invests to obtain a reward; see Korb et al., 2020), one indicator might be sufficient, provided the situation poses the same functional challenge in each species. Where the construct is defined by a broader social function, as in the case of competitive behaviour with its consequence of securing precedence at others' expense, a single behaviour captures only one of the routes to that consequence, and

several behaviours that share the function should be observed. For example, competitiveness might be assessed through displacement, threat displays, resource defence, and contest initiation. These indicators can then be combined into one variable, and the rules for aggregation should be specified a priori and justified by the shared consequences of the behaviours. In our framework, behaviours belong in one variable if their typical consequences are comparable. Such a variable is formative rather than reflective, so its indicators need not be interchangeable or correlate highly across individuals within a species.

The aggregation described above results in individual differences in competitive behaviour in one particular situation. How such variables are combined across situations depends on the property under comparison, that is, whether the target is an average level, a response to a social or ecological gradient, or the consistency of behaviour itself (see also Kuper et al., 2026). If the target is a social trait, that is, a consistent difference in average level, the values are averaged across situations, for instance to relate trait competitiveness to reproductive success. This aggregation is necessary because psychological research has shown that single behavioural observations are unreliable indicators of a construct, as a behaviour observed once reflects both the external situation and the individual (Epstein, 1979, 1983). Averaging need not extend over all situations. Observations can, for example, be restricted to specific situations (e.g., those in which a specific situational trigger is particularly strong). The resulting variable then describes individual differences only under that condition.

If the target is how individuals differ in their responses to a social or ecological gradient, referred to as plasticity in behavioural ecology (Dingemanse et al., 2010; Martin & Jaeggi, 2022; Stamps, 2016) and as (if-then) contingencies in psychology (Kuper et al., 2022; Mischel & Shoda, 1995), responses across situations are modelled as a function of the gradient, as when competitive behaviour is examined in relation to the number of rivals present. The resulting

contingency is itself an individual-difference variable. An individual with a high value on this variable competes considerably more strongly as the number of rivals increases, whereas an individual with a value near zero competes to a similar degree regardless of the number of rivals. This is distinct from the average level, since individuals who differ in how strongly they respond can compete equally much on average.

If the target is consistency itself (commonly quantified as repeatability in behavioural ecology), the situations are retained in order to distinguish between-individual from within-individual variation (Royauté & Dochtermann, 2021). While repeatability describes the sample as a whole, individuals can also differ in how consistently they behave across similar situations, which again yields an individual-difference variable.

For the comparison itself, the breadth of the construct, the level of aggregation, and the operation by which the variable is formed have to correspond across species, since a single behaviour in one species and an aggregate of behaviours in another are not directly comparable even when both carry the same label, nor are an average level in one species and a contingency in another. What is then compared across species are the individual differences these variables describe, usually expressed as correlations or as proportions of variance. The units in which behaviour is assessed therefore need not match. Together, these specifications determine what is being compared.

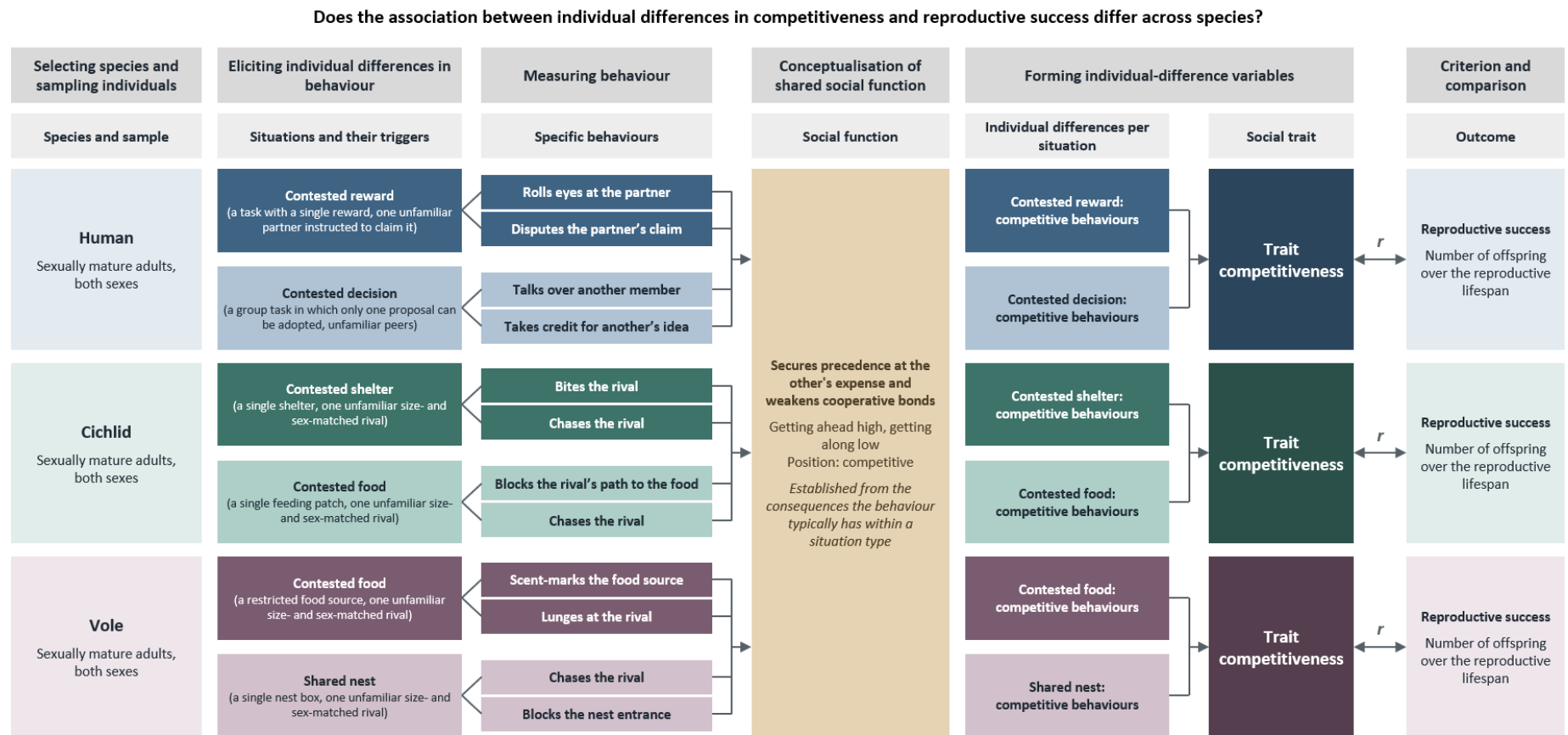
Summary and Future Directions

Cross-species comparisons offer a powerful way to ask questions about behavioural individuality that cannot be addressed within a single species. By examining whether patterns of individual variation recur across different ecological and evolutionary contexts, comparative research can distinguish patterns that are general across species, patterns that are shared among species with similar ecological conditions or evolutionary histories, and patterns that are specific

to particular species. We have focused on social behaviour because interactions with other individuals are a ubiquitous feature of animal lives, while the social environments in which those interactions occur vary enormously across species. Because individuals repeatedly influence one another's opportunities, constraints, and behaviour, their lives are linked (Kuper et al., 2025). Social behaviour thus provides a particularly informative case for comparison, in which we can ask, for example, how social organisation, social structure, mating system, and care system (Kappeler, 2019) shape the emergence, expression, maintenance, and consequences of individual differences in social behaviour. Figure 3 works through an example research question. It follows individual differences in competitiveness across three species, from species selection to its association with an outcome (in this case, reproductive success).

Figure 3

Example of a Cross-Species Comparison of Individual Differences in Competitive Behaviour



Note. The figure illustrates the conceptual and assessment decisions for one research question. In this example, all situations are constructed in the laboratory, and the behaviours shown are illustrative and not exhaustive. Sampling criteria such as sexual maturity have to be defined relative to each species.

We have outlined how cross-species comparison can be achieved by focusing on two stages of the research cycle: conceptualisation and assessment. Across both stages, our understanding can advance by integrating complementary perspectives from psychology and behavioural ecology. Bringing these perspectives together allows us to take a functional approach to comparison that asks what a behaviour does within its social context. A central contribution of our framework is to locate behaviour according to its causal role in the social interaction and to align this with established trait taxonomies, providing a common comparative reference frame even when the behavioural expressions themselves differ across species. The relevant consequences, such as securing precedence or maintaining cooperative bonds, can be examined empirically within species and used to establish the construct being compared. We consider this level particularly useful for cross-species comparison because it allows researchers to identify functionally equivalent behavioural variation without requiring the ultimate evolutionary function or fitness consequences of the behavioural variation to be known or shared across species. This does not replace an ultimate account of function. It addresses a different question and provides a bridge between behavioural expression and broader evolutionary explanations. Functionally equivalent behaviours may also rest on different mechanisms, and whether they do is a further question for comparative research. Defining social functions by their typical consequences and aligning them with an established taxonomy is one way of establishing functional equivalence, not the only one. Other definitions of function, additional or finer-grained functions, and other ways of organising them may serve the same purpose, provided they can be established empirically within each species.

Functional equivalence alone, however, does not ensure comparable measurements. The same construct may be expressed through different behaviours, elicited by different social or ecological situations, and captured at different levels of aggregation across species. Assessment,

and every step within it, should therefore be treated as a species-specific process guided by a common comparative logic, which retains the behavioural and ecological specificity needed within each species. We developed these principles for social behaviour because it is a particularly demanding case. Its expression depends on the interaction partner, and functionally equivalent behaviours can differ markedly in form across species. Yet the same logic applies to cross-species comparisons of individual differences in general, including non-social behaviour. Establishing the functional equivalence of the constructs being compared and designing assessments that capture them are essential steps towards meaningful cross-species comparisons.

Cross-species comparisons of this kind are unlikely to be achieved by individual studies or even individual labs alone, as they require specialised expertise on different species and intensive data collection. An important starting point is therefore to apply our framework retrospectively to existing studies, evaluating functional equivalence and measurement comparability to synthesise available evidence and identify recurring patterns, inconsistencies, and gaps that can generate new hypotheses (Table 3). Prospective studies could then test these hypotheses by aligning conceptualisation and assessment across species from the outset.

Table 3*Retrospective and Prospective Cross-Species Comparisons*

Aspect	Retrospective Comparison	Prospective Comparison
Starting point	Existing studies conducted independently within species	New studies designed explicitly for cross-species comparison
Scope	Functional equivalence and measurement comparability can be evaluated	Conceptualisation, assessment, and sampling can be aligned from the outset
Core task	Determine whether existing measures capture comparable social functions and whether the available evidence supports comparison	Design functionally equivalent assessments and comparable samples across species
Role of the framework	Diagnostic: identify what must hold (e.g., functional equivalence) for an existing comparison to be interpretable	Design tool: guide conceptualisation and assessment before data collection
Main limitation	Constructs and measurements cannot be changed after data collection	Requires coordinated effort, species-specific expertise, and greater investment than single-species studies
Outcome value	Identify recurring patterns, inconsistencies, and gaps, and generate new hypotheses	Test these hypotheses and provide stronger evidence on cross-species patterns in individual differences

Prospective studies would also provide an opportunity to improve how individual differences are conceptualised and measured. Psychometrics offers a foundation for establishing the link between observed behaviour and the constructs researchers seek to infer (Borsboom et al., 2004; Carter et al., 2013; L. A. Clark & Watson, 2019). For functionally defined variables, this concerns the validity of the inference from behaviour to construct, which can be evaluated within each species and, where appropriate, across species. The same applies to the transparency of the evidence on which these inferences rest. Comparative studies should document the decisions underlying species selection, hypothesis development, construct conceptualisation, assessment design, behavioural observation, and analysis, including the rationale for methodological choices and the limitations of the resulting data. Standardised reporting guidelines could support this process by making these decisions explicit and facilitating the

evaluation, reproduction, and synthesis of findings. Such reporting would also allow retrospective reviews to identify how differences in conceptualisation and measurement shape the available evidence.

These efforts would further benefit from shared infrastructure that makes behavioural data and associated materials accessible across research groups. A central platform could bring together behavioural observations, video recordings, tracking data, assessment protocols, and relevant metadata, supported by transparent quality-control procedures and expert review. The Movebank database, which provides infrastructure for managing, standardising, sharing, and archiving animal-tracking data, offers a useful precedent for this kind of collaborative infrastructure (Kays et al., 2022). Such a platform could also incorporate expert evaluations of the social function of behaviours and the characteristics of situations, helping researchers judge the comparability of existing measures and test whether measures function equivalently across species, which is rarely examined at present. Building and maintaining such infrastructure requires collaborative structures that span researchers across species and disciplines, for which initiatives that have transformed comparative research in other domains provide a model (Many Primates et al., 2019; ManyBirds Project et al., 2025). Such structures could also establish common conceptual frameworks and develop species-appropriate behavioural assessments.

Together, psychometrically informed validation, transparent reporting, and shared data infrastructure could support a more cumulative approach to cross-species research, in which retrospective synthesis informs prospective studies and the resulting evidence continually refines how individual differences are conceptualised, assessed, and compared. In this way, behavioural ecology and personality psychology could jointly move cross-species comparison of individual differences from descriptive analogy towards rigorous inference.

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