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Commentary

Sixty Years of Tinbergen's Four Questions and Their Continued Relevance to Applied Behaviour and Welfare Research in Zoo Animals: A Commentary

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Abstract: Understanding animal behaviour can feel like deciphering a foreign language. In 1963, pioneering ethologist Nikolaas Tinbergen offered a key: four fundamental questions to dissect behaviour's complexities and reduce interpretive bias. These "Four Questions" fall into two categories: Proximate (how?) and Ultimate (why?). The Proximate questions ask how the behaviour is triggered (Causation) and develops over time (Ontogeny). The Ultimate questions delve into its evolutionary history (Phylogeny) and purpose (Function). Traditionally used in behavioural ecology, Tinbergen's framework finds new relevance in fields like sentience, welfare, conservation, and animal management. This paper illustrates how further integration of these Questions into applied research can improve outcomes. For example, captive animals can receive enrichment seemingly "unnatural" in origin and form. Does such enrichment trigger species-typical behaviours, fulfilling the same adaptive function as natural stimuli would? Understanding a species' natural behaviour patterns and how the performance of such activities promotes positive welfare states is key to biologically relevant population management. Tinbergen's Four Questions can help scientists to decipher the relevance of natural behaviour, and how a species' responses to their environment indicate what individuals need and want at a specific time or place. By applying the Four Questions, we can answer this question and, in turn, refine husbandry practices and conserve behavioural diversity in managed populations. Sixty years after their conception, Tinbergen's Four Questions remain a powerful tool for behavioural research. By embracing different biological disciplines within a unified framework, applied animal zoo science will continue to advance and provide credible evidence-based outputs.

Keywords: behavioural ecology; function; phylogeny; causation; ontogeny; conservation; animal management; zoo animal husbandry

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1. Introduction

Measuring behaviour and inferring its relevance to the subject performing it has always been a challenge for those evaluating, analysing, and assessing the activities of non-human animals. To remove subjectivity, the field of ethology emerged to scientifically study behaviour in an animal's natural environment to help understand the adaptive benefits of behaviour and its evolutionary ecology. Pioneers of ethological science include Charles Darwin, Charles Otis Whitman, and Wallace Craig [1]; however, ethology as a scientific discipline emerged in the 1930s [2]. Ethology as a scientific discipline is closely associated with the works of Dutch zoologist Nikolaas Tinbergen (1907–1988), and specifically with Tinbergen's Four Questions (TFQs) that were first published in 1963 [3]. A foundational framework used to understand animal behaviour, these Four Questions provide a comprehensive approach for analysing and explaining the complexity of behaviour, encompassing both Proximate (immediate) and Ultimate (adaptive significance) factors. For example, Proximate (immediate) questions relate to the mechanisms that initiate an individual's performance of behaviour (Causation) and occur in specific circumstances over the course of an individual's lifetime (Ontogeny). Ultimate (adaptive) questions consider the selection pressures that led to the emergence of the behaviour over evolutionary time (Phylogeny), as well as its current functional consequences and adaptive significance (Function) for the species. Tinbergen built on the works of Huxley [4] and Mayr [5], whilst also engaging with critics of the ethological approach [6] to strengthen the relevance of the Four Questions to behavioural study, therefore encouraging others to use them in their research.

Together, the Four Questions enable scientists to identify the role and importance of behaviour to the individual animal (Proximate) and to the species and population more widely (Ultimate). Updates to, and re-writes of, the Four Questions have been posed to check their objectives are still fit for purposes [7–9]. By analysing the benefits and costs associated with the performance of behaviour, scientists can extrapolate why certain traits are favoured by natural selection and how behaviour will evolve in the future, as well as understand the causal factors behind behaviour (which could be especially important for evidencing best practice care for managed populations). Figure 1 provides examples of the usefulness of TFQs to deciphering how behaviour occurs, and why species perform a specific behaviour for a specific reason—this in turn provides the foundation for future research questions (both fundamental and applied). Even though there are calls for update and closer scrutiny of TFQs and what we mean by "natural behaviour", six decades later, this framework set out by Tinbergen is still considered a reliable basis for behavioural study [10] and helps unpick the intricacies and complexities that drive behavioural outputs.

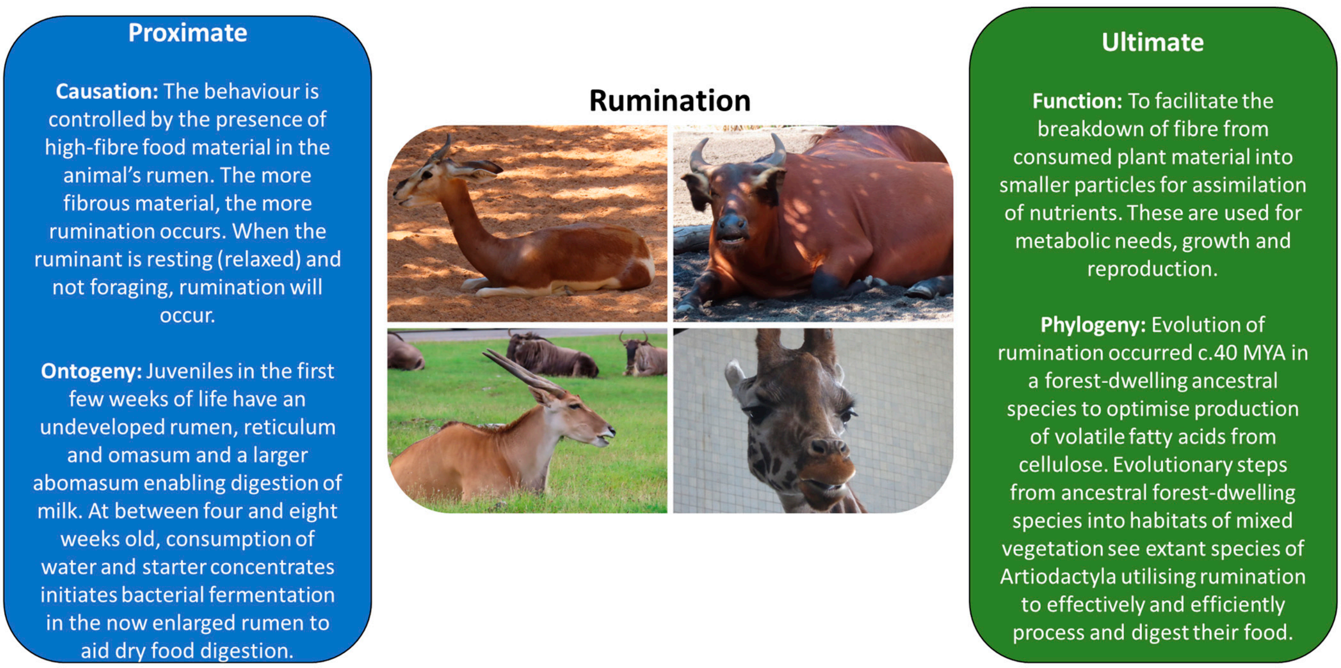

Figure 1. Applying Tinbergen's Four Questions to a specific state behaviour for a taxonomic group. In this case, the initial happens (Proximate, immediate) and end result (Ultimate, adaptive significance) of rumination ("chewing the cud") in ruminant (Artiodactyla) herbivores are shown. Four species of Artiodactyla are illustrated; Dama gazelle (*Nanger dama*), Congo buffalo (*Syncerus caffer nanus*), common eland (*Tragelaphus oryx*), and giraffe (*Giraffa camelopardalis*). Each species has a different ecology (some grazers, some browsers, some intermediate feeders) and focuses on a specific foraging niche, yet all ruminate for the same end goal. Radiation from a common ancestor, that evolved a symbiotic relationship with gut microflora to digest cellulose, has meant that extant ruminant species have diversified in morphology to enable collection of different forms of vegetation in different habitats around the globe.

In this article, we echo arguments made by others that champion the relevance of behavioural ecology generally, and TFQs specifically, to applied aspects of animal management, such as evidence-based husbandry, animal welfare, and conservation biology [11–14]. With animal welfare becoming more embedded into zoo husbandry [15] and integration of the One Plan Approach that places further emphasis on captive population relevance to species' recovery programmes [16], there is greater emphasis on animal care staff and researchers to give more credence to welfare assessment outcomes [17]. We suggest that fundamental behaviour theory is necessary for appreciating the relationships between natural behaviour, animal care, and welfare in captive settings, e.g., the links between social interactions, developments of individual social patterns, and animal welfare states [18], to advancing our appreciation of natural behaviour and why it is an essential pillar of animal care and welfare. Our understanding of fundamental characteristics and consequential appreciation of their needs (of the species within our care) is enhanced when we align information on their evolutionary history, behavioural development, and responses to humans within a TFQ framework [19]. Given the debate around the relevance of natural behaviour to how we interpret, and provide for, animal welfare states [10,20], TFQs are given further prominence in the applied scientist's toolkit for deciphering what animals do, and what animals would like to do.

2. Advancing Animal Welfare Science to Understand What Animals Need

Animal welfare science is interdisciplinary with a strong grounding in the behavioural sciences [21], and encompasses branches of behavioural ecology and neuroscience to ask how science can be used to improve animal welfare in practice [22]. Historically, the notion of wild animal welfare was given little thought amongst conservationists and animal welfarists [23]. However, a now acknowledged impact of distress (on conservation outcomes) is driving interventions to improve the welfare status of wild animals [24]. Applied behavioural data can be used to non-invasively quantify and assess animal welfare [25,26], but there is contention around all aspects of behaviour's scientific application to welfare [27]. Animals accommodated in environments that lack ecologically relevant features can display deviation from natural behaviour patterns [28] and an increase in abnormal behaviour presentation that suggests welfare compromise [29]. A species' behavioural biology must be studied to understand deviations from biologically relevant behaviour patterns when such animals are housed under human care so that the impact of such behavioural deviation can be evaluated. Appropriate inferences of an animal's welfare state can only be gained from methodologies that use a scientific perspective [30], such as TFQs. Linking behaviour to animal welfare assessment has been widely adopted in captive settings [31,32] because behavioural data provide information on the suitability of inputs that impact on animal-centred outputs (i.e., feelings and emotions that identify psychological wellbeing), and how such inputs enable animals to reach their desired goals [33]. This assists with the validation of husbandry and management practices [34,35], because such practices will be based on evidence that show animals respond to their environment and how a species' evolutionary traits need to be catered for, and demonstrate that animals are given the opportunity to behave as would their wild conspecifics [33], and this ultimately enables behavioural development that improves welfare in the zoo.

3. Opportunities and Challenges of Natural Behaviour

Individuals within a species' population perform behaviours in a specific manner, and therefore are said to display "species typical behavioural repertoires". Such behaviours have ultimately evolved based on the outcome of the action itself—the benefits gained from a positive interaction with a stimulus (e.g., successful foraging behaviour to satiate hunger) or from identification and neutralising a negative and/or harmful stimulus (e.g., escape from predation due to effective vigilance). Natural selection (a continuous process) is the mechanism by which behaviour evolves to ensure a species gains adaptive benefits [36]. Consequently, the role of behaviour within a species' life history strategy, and means of surviving and thriving, is key information that those managing populations need to be familiar with to ensure all inputs from captive care are relevant.

3.1. Outcomes of Natural Behaviour

Plasticity in behavioural phenotype is influenced by the individual's learnt responses from their environment. This in turn promotes the adaptation of future generations of species to that environment—developmental plasticity [37]—or via responses to specific environmental stimuli, where brief behavioural expression occurs, termed activational plasticity [38]. The degree of competition experienced by European starlings (*Sturnus vulgaris*) impacts on future flying abilities when adult [39], and this is an example of developmental plasticity, whereas conducting foraging behaviour whilst predators are not present [40] is an example of activational plasticity. Accordingly, an animal's behaviour is intrinsically linked to features of its environment, including interactions with conspecifics, early life experiences, and with temporal and seasonal ecological factors [41]. Thus, applying the Proximate and Ultimate perspectives from TFGs helps shed light on what drives a behaviour's performance and can evaluate its purpose.

Maintaining natural behaviours is a necessity, due to the relevance of positive behavioural outcomes that are valued by animals [42]. Husbandry and housing practices of captive individuals can be enhanced by gaining an understanding of these behavioural outputs and what elicits them. For example, knowing what an animal needs to do and what they want to do can form the basis of effective training routines and environmental enrichment programs. Although some of these behavioural outcomes may not appear natural (e.g., a lion, *Panthera leo*, pushing around a "boomer ball" in their enclosure) because the stimulus would not be present in the same manner in the wild, the outcome of the behaviour is natural as the animal will be using movements, cognitive processes, and their anatomy and physiology, to satisfy wants and needs at that specific time.

The benefits of "un-natural" husbandry protocols to enhance natural behaviour and promote healthy body condition are evidenced by the use of vertical feeding poles for large cats [43]. Understanding the developmental trajectory of wild hunting behaviour is critical to ensuring that captive-reared tigers (*P. tigris*) receive the right stimuli at the right time during maturation to maximise the chances of wild-type hunting behaviours being performed when adult. Adult tigers must be fed under conditions conducive to stimulating wild-type hunting behaviour, and since the captive environment cannot perfectly mimic the wild one, a thorough understanding of both necessary and sufficient developmental and circumstantial conditions for adult hunting behaviour is critical so that these aspects of the wild environment can be recreated [43,44]. Successful mimicking need not "look like" the wild environment. For example, feeding poles benefit behavioural aspects of welfare [44]; e.g., enhance the performance of activity associated with stalking and chasing down prey and physical health (e.g., improved muscle condition) due to reduced inactivity and lethargy [45]. A cat using a pole feeder activates and utilises the same muscular activity as a wild tiger chasing down and grappling with prey on the ground [45], so the pole promotes the usage of adaptive traits that have evolved for hunting. Tigers that use vertical feeding poles also show enhanced bone and joint health, including a reduced chance of arthroses development [44], and this would further enhance mobility and therefore the range of potential behaviours that can be expressed. This enables captive tigers to demonstrate a wider range of wild-type activities, and this has associated conservation and welfare benefits [46]. Measurement of the long-term impacts on causation and development of hunting behaviour in captive tigers exposed to a feeding pole, and how the function of the behaviour continues to be adaptive in the zoo, can be measured using TFQs.

Hypotheses that can be posed to further decipher this element of welfare-positive husbandry for tigers could be as follows:

- Do tigers refine their hunting behaviours more rapidly or demonstrate greater versatility in hunting style when they have the experience of a feeding pole?
- Do zoo-housed tigers continue to perform hunting behaviour in the same mechanical manner as wild tigers (i.e., using the same muscles and strategies for prey dispatch) when often and consistently fed from feeding poles of different heights and aspects?

- And will tigers continue to perform hunting behaviours consistently across generations in captivity due to the presence of the feeding pole even if they are several generations away from the wild?

Answering these hypotheses using TFQs would provide empirical evidence for best practice husbandry with direct relevance to tiger (and other similar carnivore) conservation, management, and the protection of positive welfare for animals under human care. The Proximate questions enable us to understand how an individual tiger is motivated to hunt and why their behavioural development occurs in the manner it does, and the Ultimate questions show us what is needed from husbandry to ensure highly evolved hunting behaviours are retained by captive populations.

3.2. Motivation of Natural Behaviours

Internal physiological processes cause a change in an animal's motivational and affective state [47,48]. Subsequent performance of behaviour can then be attributed to such changes in motivation and this is useful for determining stimuli that are being responded to [48]. In motivated behaviours, the appetitive phase generates emotions such as desire and appetite that serve to facilitate consummatory responses [49]. From consummation, satiety is achieved that promotes positive affective states, which provide welfare benefits [50]. However, unsatisfied appetitive phases of motivated behaviour can cause frustration, such as that seen during unfruitful foraging attempts by captive snow leopards, *Uncia uncia* [51], which lead to stress and poor welfare experiences. By understanding an animal's motivation, behavioural performance at a specific time of year or within specific areas of an environment gain further context. For applied study, variation in the responses of animals to different caregivers or towards different numbers of visitors can be explained by changes in motivational states. In addition to being driven by motivational cues, the impact on reproductive success can lead to behavioural shifts. That is, the mechanisms that produce a behaviour are selected due to the overall positive influence on reproductive success across a population. For example, when conflict occurs between foraging gain with predation risk, bank voles (*Myodes glareolus*) show higher levels of vigilance as a trade-off for increased foraging time [52].

Encouraging contrafreeloading—working for a reward even when a reward is easily available [53]—should be used to promote both specific foraging patterns and overall, beneficial activity across species [54,55]. Measurement of the motivation for such behaviour, how it develops across individuals, and how contrafreeloading tasks can provide for a behaviour's original function to the population can help to identify (i) if a behaviour is being lost in captive populations, (ii) how it can be re-encouraged or re-learnt, and (iii) the adaptive value of the behaviour to the population. Carefully devised environmental enrichment programs should be implemented to promote the natural function of behaviour that would be observed in wild conspecifics [56]. This, ultimately, provides opportunities for the conservation of important behaviours within captive populations. Within conservation programs for the endangered Northern bald ibis (*Geronticus eremita*), species-specific acoustic enrichment promoted reproductive behaviours, thus increasing fecundity [57] that ultimately leads to species recovery. Even after many generations in captivity, species can retain key behavioural traits important for a life in the wild, and the performance of such behaviours can be promoted by biologically relevant enclosure design or enrichment. Meerkats (*Suricata suricatta*), for example, accommodated in outdoor enclosures, still perform alarm calling and vigilance behaviour when exposed to threatening stimuli in the manner as observed in wild counterparts [58,59]. A framework such as TFQs can be used to understand how such behaviour can be promoted and maintained in populations to ensure future conservation potential.

An enriched environment (i.e., the recreation of a specific habitat or habitat feature within an enclosure) or the provision of specific enrichment items (e.g., puzzle feeders) enable the conservation of wild-type behaviours. Enrichment usage can promote adaptability to novel situations that may not be normally encountered in the zoo, either by encouraging behavioural development or reinforcing innate behaviour performance, in addition to promoting the conservation of species and their adaptive behaviours. Similarly, a population of domestic guppies (*Poecilia reticulata*) of many times over removed from wild generations perform anti-predator shoaling and inspection in the same way as wild guppies [60] when managed in a semi-natural environment. Therefore, animals under human care can remain "wild type" in their behavioural outputs—sometimes of prime importance for One Plan conservation approaches. Further study of behavioural performance over different generations using TFQs to interpret such behavioural outputs is required to evidence what facets of captive environments (and management or lack of) support the conservation and persistence of wild traits.

4. Promoting the Value of Tinbergen's Four Question to How We Understand Behaviour of Captive Wild Animals

An animal's welfare state results from subjective experiences [61], and assessing welfare via behaviour needs to be validated and replicable to ensure objectivity [62]. To understand the processes that govern animal behaviour, behavioural biologists still need to turn to Tinbergen's Questions [63]. But with a consistent and validated approach, e.g., using Qualitative Behavioural Assessment (QBA) that is a means of inferring emotional outputs from animal body language [64] or assessing personality to determine mate compatibility, behavioural measures of welfare and those of an individual's responses to husbandry are also relevant. TFQs provide a structure that facilitates and encourages interpretation of behaviour so that evidence for husbandry and housing alterations and developments is credible. For example, when providing environmental enrichment, the relevance of a behaviour that the enrichment intends to promote can only be understood based on the animal's ecology and reasons for performing such a behaviour in the first place. In this case, causation of exploratory or investigative behaviour can be linked back to the presence of enrichment; development of positive behavioural diversity (i.e., time spent on a wider range of natural behaviours) is promoted by the enrichment; the animal is able to benefit from multiple functions of behaviour (e.g., utilising different senses or parts of their anatomy) when engaging with enrichment; the enrichment is aligned to a species' specific evolutionary history and therefore enables key adaptive traits to be conserved in the zoo (for example, ensuring that primate species with an evolutionary history of tool use are able to engage in such activities in the zoo). Welfare can be improved when behavioural outputs are considered, showing that the enrichment provided is meeting each of the Four Question's explanations for behaviour in turn.

Application of TFQs is of particular importance when studying non-domestic species in the zoo to enable benchmarks for behavioural "normality" (i.e., performance of appropriate, species-specific actions within a daily time budget) to be defined. Such an approach would bring multiple benefits to understudied species in the zoo that require more research attention to help improve husbandry and welfare [65]. Multiple methodologies are used to explore behavioural ecology questions in wild species. However, external constraints placed on captive wild animals can impact the adaptive function of their behaviour, potentially causing deviation (in time, repertoire, or mechanics of the activity) from what has been observed in free-living individuals. For example, food presentation that inhibits natural foraging activity in captive African elephants (*Loxodonta africana*) also impedes the development of associated important mechanical behaviours, including gripping and manipulation [66]. This necessitates the need to apply a framework (such as TFQs) to analyse the causative agents of behavioural repertoires in captive animals, ultimately leading to better interpretation and assessment of the biological relevance of the behaviour (and what may happen when it is not performed in full or at all). Observing and evaluating how deviations from natural behaviour performance can result in welfare compromise (Figure 2) is an advantage of using TFQs within applied behaviour questions. And whilst this has been conducted for some taxa [11], we encourage a wider application across different species under human care.

Figure 2. Using the previous example of rumination, this shows how the Four Questions help to understand welfare challenges, and their persistence at the individual and population level, when a key adaptive behaviour cannot be performed and what may result in its place.

Application of TFQs helps establish best practices for zoo animal husbandry and management by basing animal care inputs on objective behavioural knowledge that considers the individual's reasons for performing a behaviour and importance of the behaviour's performance to continuation of that species' evolutionary journey. An enrichment item, even in the absence of physical interaction, may still be considered enriching if important behavioural responses are elicited [67], i.e., the animal performs a behaviour independent of the enrichment itself but this behaviour was not performed when the enrichment was not present. TFQs can be applied to understand what behaviours of importance are encouraged by such indirect engagement and inferences of the animal's motivational state subsequently made. Implementing a TFQs framework is holistic and encourages further understanding of behavioural function and therefore adaptive benefits to the animal performing it. Understanding behaviours and behavioural needs can prevent human-induced domestication of wild animals in the zoo and the maintenance of wild-type phenotypes, thus promoting the sustainability of ex situ populations [68]. By encouraging the conservation of wild-type behaviours in zoos, and the natural development of such behaviour, animals are more viable for ex situ conservation action, such as reintroduction, recovery, or population augmentation initiatives. For example, the use of puzzle feeders as food-based enrichment for golden lion tamarins (*Leontopithecus rosalia*) increased natural foraging behaviours that are essential for survival in the wild [69]. Systematic data collection can be utilised to understand behavioural development and pre-release environments conducive to wild-type behavioural outputs, as evidenced in research by Stoinski and Beck [70] on tamarins. This research involved the collection of foraging and locomotory behavioural data to determine their influence on survival rates. In turn, by establishing the age at which tamarins developed such behaviours, pre-release environments that promote their expression can be provided and thus the welfare of reintroduced animals was promoted.

5. Applying Ethology to Improve Management and Welfare of Captive Animals

This article has investigated the future relevance of TFQs to applied behaviour by considering how research/interventions concerning animal welfare, conservation biology, and animal husbandry can all benefit from a TFQ framework. We have reviewed a range of examples that show how our understanding of animal responses to the zoo can be improved when we use TFQs to identify the causal factors of behaviour and how behaviour can develop across the course of an individual's lifetime, and explain the function of a behaviour within that wider population and show how husbandry and management may alter a species' evolutionary journey. By understanding the function of behaviour in the zoo, we can promote an environment that reduces the changes of artificial, directional selection (i.e., domestication) and ensure that fitness benefits from behaviour are promoted and conserved.

As animal population managers and behavioural scientists enhance collaboration to ensure husbandry and animal care practices are evidence based and not founded on a shaky platform of anecdotes, the need for TFQs framework grows. Specific aspects of welfare-focused husbandry, such as the use of environmental enrichment, require rigorous evaluation and analysis to determine their long-term positive impact on the animals they are designed for. Many forms of enrichment are not evaluated in terms of their efficacy, the overall relevance of the enrichment to the species they are presented to, or the behavioural outcomes they are designed to promote and preserve.

Captive penguins (Sphenisciformes) may display reduced swimming and water-based behaviours compared to free-living animals [71], with associated implications for health and welfare [72]. Enrichment designed to improve swimming rates of captive penguins meets with little success, and birds either fail to engage with the enrichment or any potential benefit rapidly declines after initial interest [73,74]. Researchers should consider the evolutionary and ecological drivers for swimming behaviour in penguins to understand motivational states (or lack of) in captive birds and the reasons why they are reluctant to swim, even when encouraged to do so. Collecting data on penguin responses to humans, for example, identifies how swimming behaviour increases when visitors are absent from an enclosure [75] and this aligns with research on wild penguin behavioural physiology that demonstrates a fear response in the presence of human visitors to their habitat [76,77]. Aligning this enhanced understanding of behavioural and motivational states with the design and planning of enrichment may help enhance the overall aims of enrichment to promote specific aspects of positive behavioural diversity. Tinbergen's Proximate questions of Causation and Ontogeny elucidate why captive penguins develop restricted performance of water-based behaviours as well as clarity on how to provide causal factors to encourage such behaviours in the future. There must be consideration of natural behaviours that may be unwanted in the captive context to interpret their cause and improve enclosure design with the aim of promoting welfare. A fear response is also a natural behaviour, the same as the swimming activities that zoos want to promote in their penguins—context, interpretation, and consideration of the relevance of the natural behaviour to the animal at a given time is crucial for understanding what to promote and how to develop time activity budgets that are indicative of positive welfare.

5.1. Behavioural Knowledge to Enhance Species-Specific Management

To understand why challenges occur regarding species-specific behavioural repertoires, welfare or husbandry practice, an extension of "Tinbergian" reviews can be used to pinpoint causal factors and developmental processes that result in a behavioural response. For example, the TFQ framework can be used to understand abnormal repetitive behaviours performed in captive birds [11]. Comparative analyses of species' responses to captive environments, e.g., to understand why some species may become frustrated whereas others are likely to thrive or why some species can adapt when others appear inflexible [78,79], further support structured assessment of behaviour based on the Proximate factors and Ultimate consequences of each activity for individuals held in different captive conditions. In the aforementioned penguin swimming example, comparative behavioural study across penguin species and their responses to husbandry, management, visitor presence, and measurement of swimming time would evidence which species can perform and develop naturalistic behaviour patterns in zoos. This would allow for the construction and implementation of housing and husbandry protocols that conserve the adaptive function of the behaviour for the population, and the impact of such evidence is ultimately the potential for a population to remain evolutionarily viable from a conservation perspective [68].

Such information is beneficial to collection planning and assessment of species holdings so zoos can prioritise resources for species to be managed appropriately. Table 1 poses phylogenetic hypotheses generated from challenges that emerge in zoos, and it uses Tinbergen's Ultimate question of Phylogeny to identify what these challenges are and why captive environments and collection plans need to alter accordingly. Such an approach provides objective information for rationale decision making (e.g., on how to evolve husbandry) from applied behavioural study into a species' responses to captivity alongside of natural behaviour data from the wild.

Table 1. A question of Phylogeny used to identify why some species can experience compromised welfare when housed under human care.

Species	Phylogeny	Management and Welfare Consideration	References
Polar bear (*Ursus maritimus*)	Travelling behaviour over large home ranges requires an itinerant lifestyle to cover vast home ranges. This results in the animal experiencing novel stimuli on a regular basis. Such behaviour has evolved to utilise a hunting niche across the shifting ice flows of the Arctic circle.	Stereotypic pacing behaviours, as well head bobbing and weaving, are common in captive polar bears where captive environments do not provide for motivations to travel and range.	Bandeli et al. [80] Shepherdson et al. [81]
Killer whale (*Orcinus orca*)	Long lifespan is tied to a complex social system of family relationships and matrilineal leadership that enhances offspring survival. Such behaviour has evolved to pass down information on hunting strategies and foraging patches between kin.	Compromised physical and psychological wellbeing leading to poor survivorship and reduced lifespan compared to wild limits.	Ford [82] Jett and Ventre [83]
Gorilla (*Gorilla gorilla*)	Time spent on foraging and ingestion of plant material can take up nearly three quarters of a wild gorilla's time activity budget. Prolonged feeding times have evolved to maximise collection of nutrients and energy from plant material (that is high in structural fibre and low in energy density).	Abnormal regurgitation and reingestion (R/R) of food items is performed by captive gorillas where foraging times are markedly shorter than what has been documented in wild animals. Such R/R may cause physical health challenges and indicate poor psychological wellbeing.	Hill [84] Lukas [85]
African grey parrot (*Psittacus erithacus*)	African grey parrots flock together at feeding sites and utilise a heterogenous network of different habitat types of select food. Wild parrots consume a range of different seeds and nuts depending on season. These behaviours have evolved to maximise opportunities for social integration (e.g., for selecting a partner) and to forage optimally across the African rainforests.	A lack of companionship, limited to no opportunities for flocking, results in social deprivation. A lack of complex foraging opportunities and limited manipulation of food with the bill and foot increase time being inactive, which can then be directed to abnormal feather damaging behaviours.	Tamungang et al. [86] Greenwell and Montrose [87]
Moorish idol (*Zanclus cornutus*)	This species of fish has a complex social system where it may school for some parts of its life and then become territorial. Moorish idols roam over large areas of coral reef systems due to their specialised diet of specific sponges and algae. A flexible social system may have evolved as a response to the abundance of food and a need to defend a limited, valuable resource.	Poor survivorship in captive environments due to lack of swimming space, inappropriate diet and therefore a husbandry system that does not enable travelling and foraging actions to be completed.	Lorenz et al. [88] Dodds [89]

The complexities associated with understanding compromised welfare and why some species may appear to not thrive under human care due to the challenge of recreating outlets for important adaptive behaviours when housed in human-created environments is evidenced by Table 1. TFQs can pinpoint what the species needs to respond to, or what the function of the behaviour is, to then evaluate what is missing from the environment and make an informed decision on how to alter the situation or where is best to manage (or conserve) the species in the first place. The basis for objective and species-relevant applied behavioural study for individual under human care can be supported through assessment of how free-living individuals are affected by aversive stimuli. For example, in wild Brazilian reef octopuses (*Octopus insularis*), stress-related changes in coloration lead to increased detection by predators and reduced limb integrity that can be detrimental to effective foraging [90]. Extrapolation of such ecological knowledge to the zoo enables caregivers to accurately answer the following questions: how stressed is a captive octopus by human presence, or by handling, or from interactions with other species in the same enclosure? Further application of TFQs provides objectivity—the ecology of this species means it is stressed because of X factors it has not evolved to cope with; this species develops specific behaviour patterns that are compromised by the following areas of in-zoo care; to thrive in the zoo, populations of this species need to be provided with *X*, *Y*, and *Z* that promote the function of *A* behaviour.

Integration of ex situ (e.g., zoo-housed) populations with in situ (i.e., wild) populations is an essential principle of the One Plan Approach to Conservation as advocated by the IUCN's Conservation Planning Specialist Group (CPSG) [91]. Therefore, creating captive environments that conserve adaptive behavioural traits and designing and implementing environmental enrichment to prepare captive animals for a life in the wild provides further relevance for the continued application of TFQs to how we address causal and developmental factors of behaviour patterns, and how we understand the importance of conserving a behaviour's function across generations. Ex situ populations can be powerful conservation tools for their free-living compatriots, either directly by providing individuals for release, population augmentation or translocation, or indirectly by advocating and promoting a species' conservation needs and challenges, or by being proxies for the trialling of research projects or interventions that ultimately benefit free-living animals [92–94]. Research has identified the need for continued study of techniques, such as enrichment, for the conditioning of captive species used for reintroduction and translocation initiatives [95]. Similarly, measuring behavioural type ("personality") in zoo-reared individuals destined for a life in the wild helps to identify personality traits that will promote survival. An increased propensity to be exploratory is particularly conducive to improved survivorship [96] and social context will influence neophobia and the potential for movement into new areas [97]. Studies of behavioural types displayed by social species in captivity have revealed that assortment occurs according to an individual's personality characteristics, e.g., more aggressive flamingos (Phoenicopteriformes) prefer to assort together and offer each other social support [98]. Therefore, individual animal behavioural types will mediate and influence both their own time activity patterns and range of behaviours performed as well as those of their conspecifics. An animal's personality has fitness consequences [99], impacting how this individual can compete with others, access resources and breeding partners, and evade predation. Therefore, conditioning animals using directed enrichment to promote the performance of behavioural traits that will enhance survival, as well as identifying individual personality types (and how such different personality types interplay), will enable population managers to construct reintroduction cohorts of mixed personalities types but of individuals that have all experienced opportunities to develop behavioural survival skills. TFQs can be useful in by enabling enquiry into how different personality types respond to specific causal factors, or how different personality types develop a behaviour's performance over time, for example. Understanding the function of an abnormal behaviour (e.g., how such a behaviour may help an animal cope with an impoverished environment) to different personality types could also be a role of TFQs in the zoo.

5.2. Aligning Management with Biological and Behavioural Traits

Providing captive animals with challenges, by presenting them with problem-solving opportunities that enable the development and use of cognitive abilities, is a further aim of biologically relevant environmental enrichment [100]. Challenging animals to learn new skills, or to complete a problem using novel behaviours, encourages resilience and an ability to better cope with further, potentially more important environmental challenges in the future [101]. TFQs can allow for objective assessment of such a positive challenge by providing a mechanism for the study of behavioural control when a complex enrichment (that needs solving) is present, of development of novel actions or learnt responses to help solve the challenge, and to determine the function of such enhanced behavioural diversity to the individual and the species overall, and show how this can have an evolutionary potential that extends the conservation relevance of the species when kept under human care or in a managed situation.

Captive animals that are involved in fundamental (basic) science questions help to extend our knowledge of species-specific traits and the evolutionary reasons for their development. In turn, this knowledge should be applied to husbandry and management to ensure that species can engage and interact with the environment provided under human care in a biologically relevant manner. For example, research on binocular vision and foraging behaviours of ducks, geese, and swans (Anseriformes) has identified that challenges of food collection in different terrestrial and aquatic habitats and differences in body mass are the key drivers of differences in the horizontal and vertical binocular fields (respectively) of Anseriformes species [102]. Understanding how birds see, from what angles and distances, informs (amongst others) training programs, the specifications of enclosure design, and how to harmoniously integrate different species into mixed taxa exhibits. This research has provided valuable information on how Anseriformes perceive the world around them, and we get a better understanding of how they control and develop their behaviours accordingly. Such knowledge needs to be applied to enclosure design to ensure that resources (e.g., perching, food dispensers, enrichment devices) can be utilised effectively, exhibit boundaries and barriers are visible, and birds can navigate and manoeuvre around an enclosure's furnishings and structures safely. A TFQs framework can then be applied to specific behaviours (e.g., foraging activity within an enclosure area) to collect data on how each species performs such behaviours (when, how often, variation in performance) to ensure the enclosure aligns with a species' evolutionary adaptations.

To promote and protect animal welfare under human care, such fundamental data on anatomy, physiology, morphology, and the associated correlates of sensory perception, life history, and information processing need to be collected across taxa and then applied to husbandry, housing, and management plans. For example, sensory capabilities, including vision and olfaction, influence species perception of enclosure complexity, which can vary spatially and temporally [103]. Therefore, accounting for such differences allows for careful planning of factors that will impact on how species can utilise and experience the enclosure, and their subsequent welfare experience. For example, in multi-taxa exhibits, the placement of feeding areas or other important resources that are valuable and highly sought-after by all enclosure residents needs to be based on knowledge of how each species collects and uses information from their environment. Differences in sensory capabilities may provide an advantage to some species at the detriment of others, and therefore single-species enclosures (designed and furnished based on the sensory ecology of that particular species) may be more appropriate to the attainment of long-term good welfare. Assessment of the behavioural responses of the animals to such science-based management can be performed via TFQs, and alterations made possible accordingly to our inferences of a behaviour's meaning and the context of its performance. Using TFQs to understand the individual and species-level importance of different behaviour can assist with planning and implementation of welfare-focused husbandry—a concept that encourages the inputs provided to an animal, as part of its daily care, to be completely based around natural history, behavioural ecology, and evolutionary biology [34].

5.3. Learning What Animals Want and Need

Forthman and Ogden [104] postulated that incorporating a stringent experimental design for behavioural observations ultimately improved our understanding of species-specific environmental interactions. Integrating knowledge from different disciplines of animal behaviour research (such as behavioural ecology, biological psychology, comparative zoology) into these applied contexts allows those managing species to create enriching and welfare-focused environments that provide for an individual's behavioural wants (the animal wants to engage with an environmental or social feature, or perform a particular action of its choosing) and needs (the animal has a physiological, psychological, or evolutionary drive to perform a specific behaviour and this will still be there even if the environment is poor). TFQs continue to hold relevance and application to contemporary applied animal behaviour, especially in the context of managing ex situ populations where policy requires animal welfare to be a key consideration [105,106] and for deciphering potential welfare challenges in captive populations [11]. Understanding the immediate stimuli that trigger specific behaviours in zoo animals is crucial for their management. By identifying the physiological and environmental factors [107], social interactions [108], or sensory cues [109] that influence behaviour, animal care staff can create suitable conditions to promote biologically relevant behaviours, reduce stressors that might lead to abnormal repetitive behaviours, and design husbandry regimes alongside of an animal's wants and needs. For example, biologically relevant manipulation of environmental variables at, in, or around zoo animal enclosures could promote the performance of adaptive behaviours. This, in turn, benefits both zoo staff and visitors as both parties can (dependent on the type of behaviour being performed) more easily observe natural behaviour patterns of the animal as the environment actively facilities species-typical activity patterns. Even for less obvious or visible behaviours (e.g., food caching or hiding), visible signs of activity (e.g., disturbance to enclosure areas or movement of objects) indicate the animal has been engaged with their enclosure's features. Table 2 provides examples of how using TFQs helps those working with animals to gain new insights into how behaviour arises, and why behaviour matters (to the individual and to the population), resulting in more appropriate husbandry and conservation or welfare-focused decisions.

Table 2. TFQs applied to four areas of applied animal behaviour and how such application can improve or enhance desired outcomes.

Applied Concept	Considering Tinbergen	Relevant Outcome
Mate choice in conservation breeding	Factors that control the performance of courtship display.	Improved pair compatibility and viability of young.
	The conditions an individual needs to develop a complete courtship display to be attractive as a potential partner.	Improved strength of pair bonding and compatibility that better supports successful reproduction.
	Conserving the function of the courtship display to ensure future generations can complete such behaviour and their signals are recognised.	Individuals within the zoo continue to perform key behavioural traits that make them suitable candidates for conservation action.
	Manipulating the animal's environment so that behaviour continues to be adaptive and any artificial selection for a captive environment is minimised.	Improved reproductive success that includes managing behaviour within conservation programs and enabling animals to use sexually selected traits when part of ex situ breeding initiatives.

Table 2. *Cont.*

Applied Concept	Considering Tinbergen	Relevant Outcome
Environmental enrichment	The enrichment is designed to elicit a behaviour of importance by providing recognisable and ecologically relevant stimuli.	Enhanced time activity budgets. Improved positive behavioural diversity, and better physical and psychological health of animals under human care.
	Interactions with enrichment develop key skills in the animal over time, e.g., motor control, cognitive functions, or positive behavioural diversity.	Individual behaviour patterns are more diverse, meaning opportunities for behavioural flexibility and resilience (beneficial to buffer against short-term stressors) occur.
	The enrichment is species specific and provides an outlet for a behaviour's function that may be lost in an otherwise static environment. Similarly, enrichment can be tailored to encourage the performance of behaviours (e.g., prey selection) in captivity that are required for conservation purposes.	Enrichment promotes use of adaptive traits, including different anatomical and morphological characteristics. The animal is fitter and physically stronger, and is likely to be mentally stronger. Improvements to body condition and fitness are relevant to future conservation action.
Positive reinforcement training	Knowledge of what initiates a behaviour forms the basis of the commands provided for training regimes that an animal will participate in.	Improved engagement with training by the animal as the behaviour being trained is ecologically relevant to the animal. Wider ecological relevance of the outputs from training (for the animal and their caregivers).
	Understanding how a species develops and what cues are required for a behaviour to be performed in full (and at what life stage) is essential for complete engagement with training.	Individual animals develop more diverse behaviour patterns, are less stressed by husbandry and gain more agency over their environment. This in turn can lead to improved reproductive viability, improved health, and a longer lifespan in the zoo.
	Knowledge of a species' behavioural ecology means that mechanics of a trained action are ecologically relevant and the species will still perform important behaviours with an adaptive function resulting in domestication to a human-created environment.	Implementation of training regimes that can become the outlet for important adaptive behaviours to ensure such behaviours are not lost in ex situ populations.
Population management and translocation	Identification of causal factors of social interactions.	Our understanding of aggression or positive affiliation is improved, and social groups can be manipulated accordingly (e.g., based on when specific social behaviours may be triggered).
	Understanding how social behaviours develop at specific points of an individual's life stage and behavioural development.	Improved integration of individuals into a new group. Better knowledge of potential triggers for aggression or dominance and knowing when to intervene should such occurrences become too extreme for a confined captive environment.
	Gaining insight on the function of a species' repertoire of social interactions within a current context, e.g., the role of aggression or hierarchy. Providing an environment that is conducive to the relevant performance of social behaviours so that individuals are comfortable and connected within their social groups. Ultimately, resulting in a stable social system that is conducive to breeding.	Improved management of social groups for long-term population sustainability. A social group can be managed so that the constituent members of the social group replicate what an individual would experience in the wild, thus the function of a species' social behaviour is promoted and the adaptive benefits of being social are maintained in the zoo.

TFQs enable us to better understand concepts of distress, defined as "a state in which an animal cannot escape from or adapt to the internal or external stressors or conditions it experiences, resulting in negative effects on its well-being" [110], and which may be a part of animal welfare assessment tools. If welfare is the state of the individual as it attempts to cope with its environment [111] and distress occurs when an animal is not coping, it is essential that any behavioural inferences come from a place of knowledge of the species' evolutionary biology and behavioural ecology. Perception of animals' needs and wants can be clarified by use of species-relevant preference testing, where behavioural data are interpreted based on an animal's choices for specific interactions within their prevailing environment [112]. An individual's physiological responses to an enriched environment can reveal elevated glucocorticoids and other markers suggestive of elevated stress [25], yet this physiological response may be indicative of positive arousal and excitement. However, context is essential. For example, in adult stumptail macaques (*Macaca actoides*), the provision of novel enrichment increases faecal glucocorticoid metabolites and anxiety-like behaviours due to the unfamiliarity and stress associated with the enrichment [113]. Therefore, knowledge of natural behaviour patterns plus individual animal idiosyncrasies and personality traits is essential to any correct interpretation of a potential stress or excitatory response. The collection of behavioural data alongside of physiological measures allows for identification of arousal and excitement and provides confidence in inferences of enhanced welfare.

Comprehension of a species' ecology is key to the correct identification of actual or potential negative welfare. For example, inappetence and loss of bodyweight in incubating birds, as reviewed in Dawkins [114], could jeopardise welfare. This may occur due to competing motivational states. For example, despite an increase in other motivational states, such as foraging to satisfy hunger, brooding behaviour continues in female great tits (*Parus major*) to ensure that the desired behavioural outcome (hatching of eggs) is achieved [115]. As a result, the overriding desire to brood could compromise welfare that could necessitate veterinary or animal health intervention within a managed setting. The conundrum here is to enable the highly motivated behaviour to continue (brooding) whilst ensuring the animal does not suffer. Using TFQs within zoo breeding programmes can therefore decipher how and when a species wants to breed and why breeding may fail (is the individual sufficiently experienced or mature in their behaviour patterns, for example?).

Insight into how behaviour develops within an individual's lifetime enables management to be tailored according to an individual's needs and competencies. Understanding the Proximate mechanisms of behaviour is integral to the successful development of positive reinforcement training techniques to shape desired behaviours (e.g., operant conditioning), making medical procedures and husbandry tasks less stressful for both animals and staff. Early life experiences and socialisation leave lasting impacts on an individual's behaviour [116], so providing an enriching and a stimulating environment from a young age can lead to better-adjusted animals in terms of how they cope and respond to a managed environment under human care. For example, Linnaeus's two-toed sloth (*Choloepus didactylus*) housed in walk-through enclosures are more susceptible to stress that causes reduced foraging behaviour [117]. Elevated stress may suggest that such an environment is not suitable for the species, and therefore a more appropriate enclosure providing reduced noise pollution and refuge would benefit the animal. TFQs can be utilised to indicate the needs and wants of an animal and support the development of management strategies to account for these effectively.

Knowledge of the adaptive significance of behaviour within a managed setting is essential for the promotion of overall positive animal welfare states and mental stimulation. Animal care staff strive to replicate behavioural function within the confines of captivity by, for example, providing opportunities for foraging, exploration, and social interactions to meet species-specific behavioural needs. Providing animals with the opportunity to sate a motivational choice, even when not acted on, can benefit welfare [67]. For example, enabling Amur tigers (*Panthera tigris altaica*) with the choice to move freely between enclosure areas decreases inactivity and promotes a wider range of species-typical behaviour patterns [118]. Considering the evolutionary history of behaviour when designing an enclosure or when writing management guidelines for a zoo-housed species builds ecological relevance into the environment created for the species, and this enables a behaviour's adaptive potential to be conserved. For example, morphological [119,120] and behavioural [121,122] differences are known to occur between free-living and captive-bred individuals of different species. Such changes to morphology and behaviour would compromise wild survival and reproductive potential. Information on the causal and developmental factors of such morphological and behavioural deviations, as well as on any long-term implications on behavioural function and evolutionary potential, can be implemented in animal training programs, enrichment schedules, enclosure design, and management plans to ensure the size and shape of physical features, and the time spent on key behavioural outputs, equates to that observed in free-living individuals. Therefore, the role of TFQs in evaluating the relevance of husbandry (to the individual animal and the population overall) is clear—each element of husbandry and the behavioural outcome influenced by it can be considered against TFQs to determine the suitability of management regimes for that individual, species, and population.

The conservation of behaviour is as important as the conservation of genetic potential. Therefore, information on Function and Phylogeny provides evidence for how to promote key adaptive behaviours under managed conditions. For example, conspecific communication in some zoo-housed species, including meerkats, is influenced by the generational gap between captive and wild animals [123]. Therefore, encouraging exposure to threatening stimuli (yet in a controlled setting without an actual predation event) in zoo animals that elicits a natural anti-predator behavioural response, such as alarm call vocalisations, promotes conservation of the behaviour. Such interventions help ensure that behaviours with an adaptive function, though not necessary for survival in captive populations, are maintained through the retention of knowledge, thus closing a generational gap between wild and captive conspecifics.

Across conservation behaviour disciplines, for example, in Buchholz [124], applying behavioural methods to other aspects of species or population management interventions can promote positive outcomes and aid in finding solutions to challenges. Adaptation and evolution of TFQs have been called for [10,125], particularly for scientists to better understand the evolution of both species as entities and of their specific behaviour patterns [126]. Further scrutiny of the application of TFQs to the study of behavioural development and zoo animal welfare states, to determine the best possible care for managed animals [10], should be regularly conducted to ensure that research outputs are valid, relevant, and robust. Some authors have suggested refining and rationalising the concept of the Four Questions into "causes", which would include Causation, Ontogeny, and Phylogeny, and "consequences", which includes Function [8]. Another approach could be to consider "causes, structure and consequences" of behaviour along a continuum [9]. Authors argue that such developments to the original TFQs would rationalise and better explain relationships that exist between the questions and provide more nuanced reasoning for how and why behaviour occurs. Ultimately, however, TFQs remain a relevant framework for either designing and implementing research specific to the collection of natural behavioural data, as well as a way of considering what could be gained by an additional behavioural element into a multiple-dimensional project (e.g., conservation biology, animal welfare, or biological psychology) to enhance the impact of the research more broadly. Criticism of some animal welfare concepts as lacking in validity, repeatability, and utility [127] adds further weight for continued usage of the Four Questions framework that is objective and clear in how the questions consider the complementary levels of analysis of behaviour (which can then be used to better understand the relevance of zoo husbandry and its impacts on animal welfare).

6. Conclusions

Research that investigates applied animal behaviour questions is critical to the continual development and evolution of animal management, animal welfare assessments, and species conservation outputs. The principles and practices employed to manage animal populations under human care need to be evidence-based on strong foundations of behavioural ecology, natural history, and on information collected from the individual animals themselves to understand their wants and needs. Not all the stimuli that animals will respond to will be natural; however, the underlying cause of their response to such stimuli and mechanics of the behaviour that will be performed is natural. Evolved traits assist the performance of adaptive behaviours and animals continue to perform specific actions that provide a reward most effectively (e.g., satiate hunger or remove themselves from threat).

Although now 60 years old, TFQs continue to provide a valuable and practical framework for applied animal behaviour in managed settings. We encourage future research questions that look within a taxonomic group to identify and evaluate the Proximate and Ultimate factors behind adaptive behaviours whose performance is clearly important (both physically and psychologically) to the individual. For example, deviation from natural behaviours, such as rumination in Artiodactyla, may cause an increase in abnormal repetitive behaviour performance that can indicate negative welfare. We also believe that Tinbergian reviews [11] are extremely useful to how we advance zoo animal management protocols. Such reviews help us recognise challenges in animal welfare (for example) and provide general (to the population) and specific (for the individual) changes to the environment or to animal care that promote the performance of key behaviours. The scope of a Tinbergian review should be extended across all taxa, starting with those that we are already aware of as being challenging to manage or cater to under human care. It is essential that natural behaviour is not ignored in applied animal science, animal management, animal welfare, or in conservation biology for it is the foundation of what a species has evolved to do to live and reproduce and adapt for the future. Ensuring animals can express adaptive behaviours enhances their role and value within their specific zoos and thus further underpins the relevance of TFQs to evidence gathering for 21st century animal husbandry and management.

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