

Tinbergen's four questions: an appreciation and an update

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This year is the 50th anniversary of Tinbergen's (1963) article 'On aims and methods of ethology', where he first outlined the four 'major problems of biology'. The classification of the four problems, or questions, is one of Tinbergen's most enduring legacies, and it remains as valuable today as 50 years ago in highlighting the value of a comprehensive, multifaceted understanding of a characteristic, with answers to each question providing complementary insights. Nonetheless, much has changed in the intervening years, and new data call for a more nuanced application of Tinbergen's framework. The anniversary would seem a suitable opportunity to reflect on the four questions and evaluate the scientific work that they encourage.

Origins of Tinbergen's questions

In a famous paper dedicated to Konrad Lorenz on his 60th birthday, Niko Tinbergen [1] recognised that biologists working on behaviour focus on different types of problem. Some want to know, for instance, how the expression of a particular character is controlled, whereas others want to know how it benefits the organism. Tinbergen pointed out that four fundamentally different types of problem are raised in biology, which he listed as 'survival value', 'ontogeny', 'evolution', and 'causation'. These problems can be expressed as four questions about any feature of an organism: what is it for? How did it develop during the lifetime of the individual? How did it evolve over the history of the species? And, how does it work? Although Tinbergen was concerned with behaviour, the four questions apply broadly to any characteristic in living (and even some nonliving) systems. For instance, traffic lights could be thought of in terms of how they were assembled, how their design evolved over time, how their use increases the chances of survival of road users, and how they work [2]. In the case of a fully formed feature of an organism, including any aspect of its behaviour, the biological function and mechanisms of control are current problems, whereas individual development and evolution are historical.

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Attempts to delineate logically distinct ways of understanding a character date back to Aristotle's classification of causes. Tinbergen's article [1] followed shortly after Mayr's [3] distinction between proximate and ultimate causation, and Tinbergen's 'survival value' and evolutionary issues have often been characterised as 'why questions' and mechanistic and developmental issues as 'how questions' [4], although, confusingly, the four problems are also often called 'Tinbergen's four whys'. However, Mayr's deployment of 'ultimate causation' was ambiguous, simultaneously seeking to encapsulate both the 'function' of a character and its 'evolutionary history' [5], and problematic because 'ultimate cause' is frequently equated with function, which is not a cause [5]. By contrast, Tinbergen's formulation has the advantage of clearly distinguishing between past and present, as well as function and cause. Tinbergen credited Julian Huxley [6] for his distinctions between causation, survival value, and evolution and then added the fourth problem, ontogeny, impressed by the arguments of developmentally minded critics of ethology (e.g., [7]). Unlike Mayr's [3] scheme, Tinbergen's framework has attracted little criticism, and has stood the test of time. Indeed, almost every modern textbook on animal behaviour quotes his distinctions with approval. Notwithstanding the widespread agreement that Tinbergen performed a major service to biology, much has changed over the past 50 years, and some of these developments present challenges for Tinbergen's formulation. Here, we examine the conceptual and empirical developments that have taken place in this field and reflect on how they impact on Tinbergen's framework. We argue that the four-questions scheme remains a useful heuristic, but that it requires a more nuanced interpretation than is traditional. (For more comprehensive treatments of Tinbergen's legacy, see [8–10]).

What is it for?

Tinbergen [1] devoted a substantial proportion of his paper to investigation of the function of a character (what we refer to here as its 'current utility'), because he felt that this aspect of ethology had been neglected. Tinbergen's own research group showed how hypotheses about current utility could be tested through experimentation [11], and he would no doubt have been delighted to see how his pioneering work has blossomed into one of the most vigorous and productive fields of behavioural biology, and the dominant concern of behavioural ecologists (see [12]).

Unfortunately, the notion of biological ‘function’ causes confusion because the word has many different meanings (such as the physiologists’ use for the workings of a structure). Many biologists prefer the term ‘adaptive significance’ because this clearly relates the functionality of the characteristic to its contribution to fitness. For Tinbergen, fitness was largely related to survival, but this is supplemented in modern parlance by reproductive success and the contribution of the characteristic to its likelihood of appearing in subsequent generations, as captured by Hamilton’s concept of inclusive fitness [13]. However, we prefer the term ‘current utility’ to ‘adaptive significance’, because it helps to emphasise how the current and original function of a characteristic can differ, and because it makes no assumption about the processes that generated the functionality. This is more than just a terminological issue, because extensive evidence shows that characteristics change function over time (e.g., feathers that evolved for temperature regulation but were adapted for flight); indeed, one of the primary messages of evo-devo research is that evolution frequently proceeds through the co-option of existing characters [14]. Moreover, developmental processes can generate functional phenotypes (‘facilitated variation’), often through exploratory processes, the final form of which is not pre-specified [15]. In other words, rather than fashioning a particular character, animals often have capacities to respond flexibly to local condition with adaptive responses, many of which are themselves knowledge-gaining processes [15,16]. A good example is characters fashioned by cultural evolution, which is now known to be widespread in animals [17] (see below). These findings imply that researchers need to be mindful that current utility need not equate with original function, and that functionality need not be the direct product of natural selection.

The precise way in which a characteristic increases fitness is often described in terms of its apparent design. The perception that a character is designed springs from the relations between the characteristic, the circumstances in which it is expressed, and the consequences of its expression. Unfortunately, pre-Darwinian ideas about intelligent design have been appropriated by the creationists seeking scientific respectability for their beliefs, leaving many biologists who are not creationists reluctant to use the term. In some fields (notably, behavioural ecology) the word ‘design’ is used commonly because researchers relate it to the view that natural selection has led organisms to behave as if maximising their inclusive fitness [18]. However, leaving aside any misunderstanding generated among the public through such terminology, substantive scientific concerns are only now starting to be realised with the recognition that apparent design can be derived in many different ways, such that its detection need not imply adaptation, or even selection. The opening of milk-bottle tops by tits is a good example of a well-designed behaviour pattern that is not the direct product of natural selection.

These issues have been more extensively considered with respect to the concept of ‘adaptation’, which is commonly thought of as the fit between a characteristic and a challenge set by the environment, but is also subject to confusion because adaptation, apart from its physiological

meanings, is also the term used for the major process by which the fit is achieved (i.e., natural selection for the characteristic), and many evolutionary biologists reserve the term ‘adaptation’ for characters fashioned by natural selection for the functionality attributed to them [19]. The important point here is that the semblance of design is observed in ‘exaptations’ [20], ‘spandrels’ [21], and can result from a cultural evolution process [17,22]. A failure to recognise such alternatives perpetuates a vulgar form of adaptationism [21]. In principle, confusion over ‘function’, ‘design’, and ‘adaptation’ can be obviated if a clear distinction is drawn between current utility and the historical processes by which its current state was reached, as Tinbergen advocated. Nonetheless, these terms continue to be used in different ways [23], frequently with strong assumptions being made about the historical processes responsible. Researchers should remain alert to the point that it is easier to show that a character enhances survival and reproductive success, thus determining its current utility, than to establish that it evolved for a particular function [24,25].

How did it develop?

Although Tinbergen is credited with stimulating research into behavioural development through his inclusion of ontogeny in his list of problems, he himself carried out little research on this topic. However, developmental ethologists and psychobiologists (such as Gottlieb, Hinde, Hogan, Kruijt, Marler, and ten Cate) formed strong links, leading to productive investigations of topics such as attachment, filial and sexual imprinting, and bird song [26,27].

However, critical issues have arisen over what an animal inherits at the beginning of its lifetime. Tinbergen probably thought that, for most animals, it was only genes, which meant that at the time developmental processes were best viewed as starting at conception. Over the past 50 years, major developments have occurred in the understanding of extra-genetic inheritance processes, such as cytoplasmic effects, parental effects, including maternal and paternal genomic imprinting and other epigenetic impacts on gene expression, ecological legacies, behavioural traditions, and cultural inheritance [28–32]. Many of these effects are taxonomically widespread. For instance, social learning is now known to be ubiquitous in more complex animals, with thousands of reports of novel behaviour (related to diet choice, foraging skills, antipredator behaviour, etc.) spreading through animal populations through learning, in hundreds of species, including not only primates, but also cetaceans, rodents, many other mammals, birds, reptiles, fishes, insects, and cephalopods [17,30,33]. These legacies have several important implications, including that the developmental processes shaping a character will often start before conception.

Many of the factors that influence individual development, be they social or ecological, have been amassed by the activities of multiple individuals over multiple generations (cultural knowledge and ecological legacies). Some of these influences on development can stretch back a long way. The presence of animal burrows, mounds, and dams

or, on a larger scale, changed atmospheric states, soil states, substrate states, or sea states [34,35], persist or accumulate in environments, and can be crucial for normal development. Tracing backwards in time to the origins of these factors can be important to the modern study of development, particularly where those legacies function to elicit or regulate epigenetic changes in the development of descendants [36]. The spirit of the ‘ontogeny’ question pushes back the historical account of how the character developed to before conception and requires acknowledging that the variety of factors that are inherited, and the manner in which parents construct developmental environments [36], are important for developmental studies.

The Modern Synthesis was built on the assumption that inheritance could be reduced to transmission genetics, with the separation of heredity and development hailed as a major achievement [37]. However, the inheritance of species-typical phenotypes, as well as within-population differences between phenotypes, requires reference to the recurrence of nongenetic causes of development, throughout the lifetime of an animal [36]. Heredity occurs not only because of transmission of DNA, but also because parents transfer a variety of developmental resources that enable the reconstruction of developmental niches [36,38]. These findings have transformed heredity from a one-off legacy at conception to a multifaceted process that continuously shapes development throughout the lifespan.

How did it evolve?

The past 50 years have witnessed major developments in understanding the evolution of behaviour, derived through the development of sophisticated theoretical tools, such as comparative statistical methods used to construct phylogenies, as well as experimental investigations of natural and artificial selection. Despite this progress, of all the problems identified by Tinbergen, evolutionary questions have been the subject of most discussion. Tinbergen thought that the main issue was to do with how natural selection had operated in the past, providing the genetic basis for what an individual inherits. Since then, chance events, such as genetic drift and founder effects, have been recognised as important influences on what is inherited genetically. Indeed, recent findings from comparative genomics imply that drift might dominate the evolutionary dynamics of multicellular organisms [39]. What Gould [40] referred to as ‘unity of form’ sets important constraints on what can and cannot be inherited, and researchers increasingly consider the possibility of a ‘developmental bias’ acting on the distribution of phenotypes subject to natural selection [41,42]. The ontogenetic processes of self-regulation and plasticity strongly suggest that random genetic mutation will rarely mean random variation in phenotypes [14,15,41]. As mentioned above, strong evidence indicates that evolution frequently occurs through the co-option of existing systems [14,41]. Gould and Vrba [20] coined the term ‘exaptation’ for the evolutionary process by which a characteristic is co-opted to meet a new requirement set by the environment. A good example is provided by the remarkable similarity between the hiss of the burrowing owl and the rattling of a rattlesnake, which had resulted from the hiss being co-opted for

a defensive function from the food-begging call seen in other related species [43].

These observations opened the door to consideration of a more active role for behaviour in evolution, where plastic behavioural responses to environmental change impact on the evolution of the descendants of the animal and trigger evolutionary change in morphological characteristics [16,27,29,30,44–46]. A variety of behavioural factors influencing the evolution of descendants has been identified. These include choice (particularly of mates), mobility of the organism, construction of ecological and developmental niches, and adaptability [29,36,44,46–48]. Developmental processes, including learning, contribute to evolution by systematically generating, exposing or shielding the phenotypic variation that is subject to natural selection [16,29,48,49].

The recent emphasis on a role for cultural evolution in explaining human cognitive and behavioural characteristics such as language [50,51] means that, for some characters, two kinds of evolutionary history have to be recognised [25,45,52]. The question then becomes ‘which historical processes were responsible for the character?’, and ‘how can its trajectory be explained?’. This is relevant to debates over the evolution of cognition because a major issue about the evolution of language is whether particular features of language are the product of natural selection or cultural change [50,51,53]. A cultural evolutionary history can operate within the lifetime of an individual, such as linguistic changes, or over a greater duration, such as Oldowan lithic technology [52]. In such cases, clarification is needed about whether the particular impact on the behaviour of an individual is developmental or evolutionary. Indeed, whether cultural change is best characterised as evolution or development is a point of dispute among researchers studying human behaviour [45].

Given that social transmission is now known to be widespread in nature, it would be a mistake to assume, as has been common, that such complexities only apply to humanity; social transmission been found to affect the evolution of a variety of animals, in different ways. For example, mate-choice copying, where the choice of mating partner is influenced by the mate choices of other individuals, is found in *Drosophila*, fishes, birds, and mammals [17]. It propagates mating preferences over short time periods (i.e., a single season), yet population genetic models have shown that it can strongly affect the strength of sexual selection [54], whereas experimental data reveal that it generates unpredictable ‘fads’ in the characters that females find attractive [55]. Another illustration comes from studies of bird song, where theoretical models have found that song learning affects the frequency of alleles that influence song acquisition and preference [56], promotes the evolution of brood parasitism [57], and facilitates speciation [58]. A third example is the socially transmitted mobbing of brood parasites by host birds, which affects the balance of costs to benefits in the evolution of parasitism [59]. Tinbergen would have been delighted to witness how the study of behaviour has become so central to the understanding of evolutionary processes.

Review

How does it work?

In 1963, Tinbergen lamented the plurality of fields that explored the mechanistic bases of behaviour, and called for a multilevel analysis ‘ranging from the behaviour of the individual and even of supra-individual societies all the way down to Molecular Biology’ ([1] p. 416; see also [60]). The links between the levels of analysis remained relatively tenuous for many years, but more recently enormous strides have been made in understanding the molecular, neurobiological, and hormonal bases of behaviour, in linking the physiology of metabolism and behaviour, as well as integrating behaviour with the state of the immune system [61,62].

A major challenge facing scientists in this area has been to put together properties that have been isolated for purposes of experiment and yet which must be interconnected in the freely behaving animal, or complex society. An important insight in addressing this challenge is the middle ground between bottom-up and top-down

perspectives. Researchers can reach down to lower (e.g., molecular) levels, or up to higher (e.g., behavioural) levels, constraining their focus to that which is functionally important, thereby preventing them from being swamped by complexity [63]. A compelling example is the study of bird song, which boasts an integrated mechanistic understanding ranging from gene expression, through a well-mapped neural circuitry of brain nuclei and their projections, to a rich understanding of how sensory inputs elicit song learning and production [26,27,64] (Figure 1).

Relative to Tinbergen’s other questions, the study of mechanism has proven comparatively straight-forward, if not without challenge. However, one terminological issue deserves a mention. Tinbergen’s use of the term ‘causation’ for studies of mechanism is not ideal, because proximate causes can be traced back in time, which misleadingly implies overlap with developmental questions. A better term is ‘mechanisms of control’, which better captures Tinbergen’s intended focus on the here-and-now.

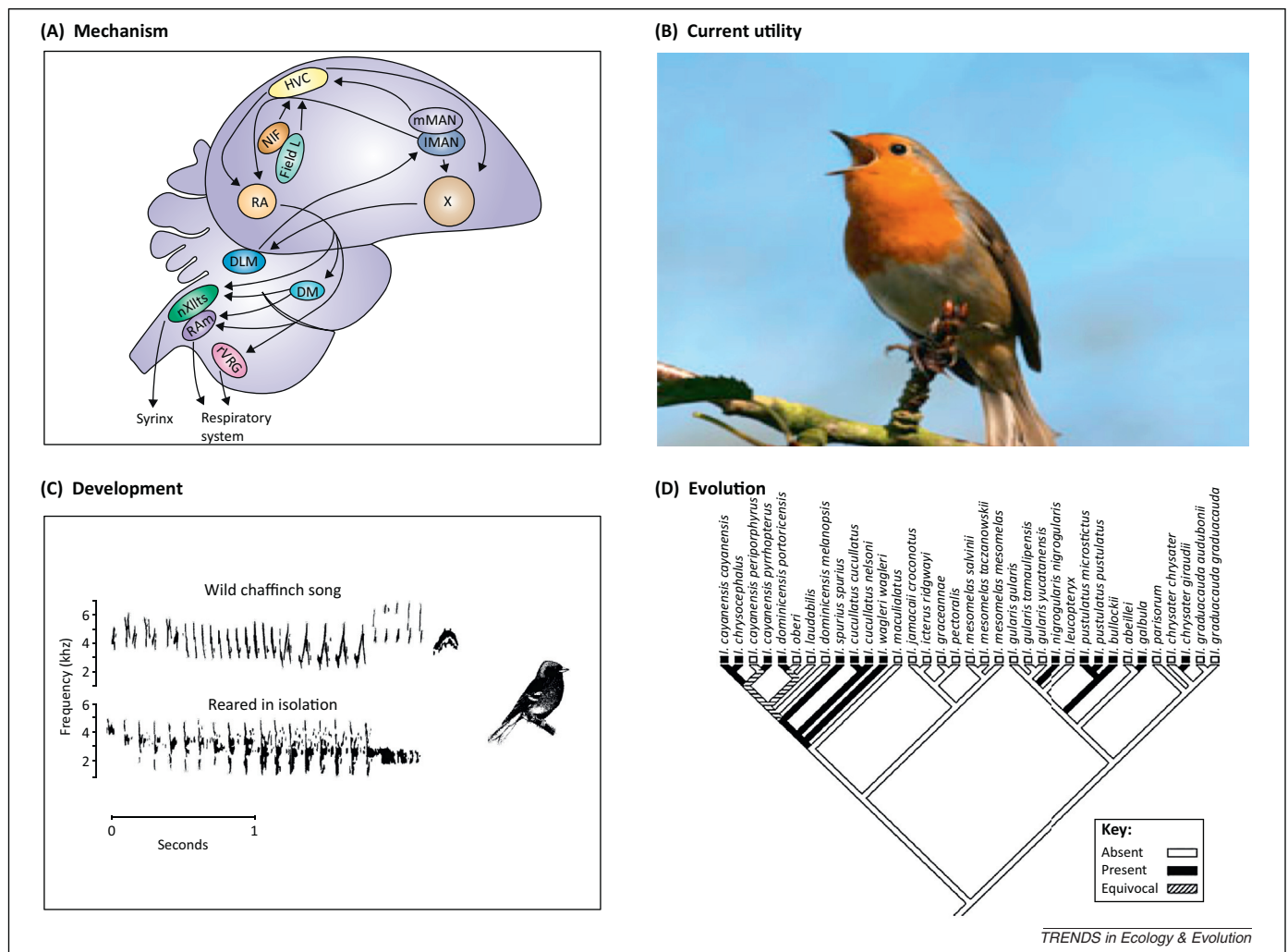


Figure 1. Tinbergen’s four questions in one system. Despite Tinbergen’s [1] emphasis on the need for an integrated understanding, in few study systems have all four of Tinbergen’s questions been addressed. One such system is bird song. **(A)** Mechanism. Researchers have amassed a good understanding of the mechanisms underlying bird-song learning and production, central to which is ‘the song system’, a well-mapped neural circuitry of brain nuclei and their projections within the songbird brain [26,27,64]. **(B)** Current utility. Birds sing primarily to advertise their quality, with songs functioning as signals both to warn off rivals and attract mates [27]. **(C)** Development. Experimental investigations, such as rearing nestlings in captivity isolated from adults, have revealed that songbirds typically learn their songs early in life. The song is learned during a sensitive period, when birds are predisposed to learn the songs of conspecifics. The image shows sonograms of a typical wild chaffinch song and of the song of a chaffinch reared in isolation. **(D)** Evolution. Comparative analyses have established that song features vary along phylogenetic lines, such as clicks in the songs of orioles [78]. Researchers have also documented how songs in many contemporary songbird populations change through a cultural evolution process in which song elements are differentially transmitted [27]. Reproduced from [26] (A) and [27] (B).

Inter-relations between the four problems

Tinbergen's questions are not the only questions that can usefully be asked about behaviour and, over the years, many candidate 'fifth questions' have been proposed (Box 1). Nonetheless, Tinbergen's questions retain a deserved prominence. Tinbergen regarded his distinctions as being pragmatic, but in many respects they are also logical: answers to any one of Tinbergen's questions cannot be regarded as also answering another [65].

The importance of this issue does not imply that each of Tinbergen's problems must be addressed alone, or that the findings of one are irrelevant to the others. On the contrary, Tinbergen felt that an important part of ethology was to bring the problems together; this point has been made many times since (e.g., [10,66,67]). In many contexts, two or more of Tinbergen's problems need to be addressed simultaneously. For instance, a growing number of examples have been found in both plants and animals of how the phenotype is radically influenced by ecological conditions, for instance, nutrition-, temperature-, predator-, light-, or stress-dependent polyphenisms [31,36,16,68]. These cases raise the question: do plastic developmental responses represent adaptations to the environments in which they are found, or is it more appropriate to regard the general capability for plasticity to be the adaptation? Different answers will likely be required in different cases. Such examples have also prompted researchers to wonder whether, and how, developmental systems fashion evolutionary outcomes, generating valuable experimental work and important insights that can only be gained through the simultaneous consideration of two questions [14,16,31,36,44,48,69].

Clearly one type of study can lead into another. For instance, fieldwork can generate hunches about what a given pattern behaviour was for, leading to ideas about the best way to solve that problem if the animal were designed

by an engineer. Here, the behavioural ecologists' focus on current utility has intersected promisingly with the experimental psychologists' analysis of animal learning (e.g., [70]). For instance, as an animal gathers information about its fluctuating environment, what rules should it use in deciding where it should feed? Ideas about the best ways to forage in different places, or type of information to rely on, provided insights into the underlying processes [66,71,72].

Although many behavioural ecologists believe that an understanding of current utility gives insights into the nature of the mechanisms [12], some authors (e.g., [73,74]) have been concerned that such 'insights' are often erroneous or misleading. The future will show whether they were right. Conversely, other researchers have suggested that knowledge of mechanism can shed light on, or constrain, current utility and argued for more mechanistic model building [75,76]. Such attempts at integration should be encouraged, even if they are not fool proof. Minimally, insights from what is known about one of Tinbergen's problems generate testable hypotheses, or draw attention to relevant evidence, for others.

Development and mechanism appear intertwined because the 'how does it (currently) work?' question requires the abstraction of an instant in time. In reality, developmental change is continuous, so a complete understanding requires knowledge of how the character works at all relevant times. Hence, mechanism always requires specification of a point in development. This difficulty was recognised by Tinbergen, who wrote: 'ontogeny can be said to continue beyond the period of growth to maturity and the causation of the behaviour of the adult animal therefore grades into that of the phenomenon usually classified under ontogeny; the distinction is partly one of the time scale involved' ([1] p. 427). In this case, a distinction between current mechanisms of control and developmental history is

Box 1. Additional questions

The problems identified by Tinbergen are not the only problems that biologists can address and, in the intervening years, many researchers have proposed additional questions to supplement Tinbergen's. Two such questions are 'How is the behaviour inherited?' and 'How can the four questions be integrated?' (see main text). A third is 'What is the character?', because any behavioural analysis needs to start by specifying what is to be explained [65]. Indeed, Tinbergen all but proposes this question himself by stressing the importance of observation and description at the outset of his article. Tinbergen wrote: 'Contempt for simple observation is a lethal trait in any science' ([1] p. 411). At that time, an aim for ethologists was to provide a complete description of behaviour for a studied species, leading to what was called an ethogram. Since then, the variation within a species and its dependence on local conditions has become increasingly apparent, leaving the construction of ethograms of questionable value. Nonetheless, the stress on getting to know their animals, so that researchers could frame sensible questions about them, was a key feature of Tinbergen ethology that remains as valid today as it ever was.

However, identifying meaningful behavioural (or morphological) units is no trivial issue, because evolutionary biologists historically have struggled to delineate the characters subject to natural selection [79], and, as Tinbergen noted ([1] p. 414), units of current utility need not be units of mechanism. Nonetheless, description of the character is important, even though the type of description can depend on the problem.

Projections from animals to humans have been common enough and subject to much criticism [80]. The anthropomorphism, rampant in writing about animal minds during the early part of the 20th century, led to the reaction by strict behaviourists and, indeed, Tinbergen's determination to create an objective study of animal behaviour. For many years, attributing human emotions and intentions to animals was regarded as illicit (see [80,81]). By contrast, emphasis on the dangers of anthropomorphism undoubtedly constrained research. From the counter-perspective, a scientist who never considers that an animal can exhibit human-like complexity can miss much of the richness of its behaviour.

The growing interest in animal awareness has encouraged evermore sophisticated studies of animal cognition (e.g., [67,82]) and has stimulated clever experiments that shed important light on animal suffering and welfare. This trend has led to the suggestion that a fifth question should be added to Tinbergen's four, namely 'Of what is an animal aware?' [83]. Thinking of behavioural outcomes as the goals of animal intentions has undoubtedly helped many researchers to deal with the complex processes that control the behaviour of an animal. However, attributing the power of thought to an animal, to do more imaginative science, does not mean that, when efforts are crowned with success, proof has been obtained that the animal thinks in the manner attributed to it. This point lies at the heart of the difference between the heuristic and the truth value of the attribution [80].

Review

pragmatic. The same is true for the distinction between events occurring before conception and those occurring afterwards.

Concluding remarks

The above considerations lead us to several practical recommendations (Box 2), designed to retain the spirit of Tinbergen's objectives but update them in the light of insights garnered over the past 50 years. Tinbergen saw a great advantage in addressing all four of his problems. He wrote: 'a comprehensive, coherent science of Ethology has to give equal attention to each of them and to their integration' ([1], p. 411). Therefore, he would have been disappointed that much behavioural work published since his 1963 paper has typically ignored studies of mechanisms of control and development. Gradually, it has become apparent that this neglect of an important part of the biology of behaviour was a serious mistake. The study of behavioural mechanism and development is important in stimulating (as well as constraining) ideas about the current utility and the evolution of behaviour.

Here, it is germane to ask what is the job that Tinbergen's four problems formulation is designed to do? Is it (i) to promote the study of all four areas of research, and due recognition that each is important? If so, then it has been successful. Or is it (ii) to generate a comprehensive and

integrated analysis in which all four necessary components are combined to generate a complete understanding of the character [77]? If the latter, then Tinbergen's scheme has less obviously been a success. In the main, Tinbergen's four questions are studied independently [10], although functional and evolutionary questions are often bracketed together, and likewise so too are mechanistic and developmental questions. In relatively few cases have all four questions been answered for a single character (bird song is one example; Figure 1). A pragmatist might respond that this is an inevitable reflection of the fact that researchers are usually focussed on a particular problem. However, Tinbergen's concern that ethology was 'in danger of splitting up into seemingly unrelated sub-sciences' implies that integration was important to him. He ends his article with a plea for a 'fusing of many sciences, all concerned with one aspect of behaviour, into one coherent science' ([1], p. 430). Although some progress has been made over the past 50 years, it is timely to urge that Tinbergen's plea be answered.

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Box 2. Practical implications

Scientific developments over the past 50 years demand a more nuanced interpretation of Tinbergen's four questions. We make the following recommendations:

- (i) A focus on current utility best begins with the question 'What is it for?', avoiding any presumption about the historical processes that gave rise to it. Researchers need to be mindful that current utility need not equate with original function, and that functionality need not be the direct product of natural selection.
- (ii) Processes highly germane to an understanding of development start before conception, and development can be influenced by transgenerational legacy effects. The 20th-century separation of heredity and development is being challenged by recent data showing that offspring inherit more than genes, and that the parental phenotype is actively involved in the reconstruction of offspring developmental niche by uptake, synthesis, and transference of a range of resources during egg formation, embryonic development, and beyond.
- (iii) A focus on evolution needs to recognise the possibility of different levels of organisation at which natural selection can act and the constraints and biases on development. It should ask which evolutionary process, and which system of inheritance, is responsible for the character. Behaviour, and developmental processes in general, are likely to have more active roles in evolution than traditionally conceived.
- (iv) Tinbergen's terminology warrants updating. 'Causation' is too ambiguous a term and Tinbergen's objectives are better captured by 'mechanisms of control'. Likewise, 'function' is better replaced by 'current utility' and relates to reproductive success as well as survival. In restricted cases, current utility can be better understood as serving a function deriving from a cultural evolution process.
- (v) Integrative solutions to the four problems are needed to generate a deep, overarching understanding.
- (vi) Although formal ethograms are of limited utility, it remains valuable to begin behavioural analyses with an observational period, designed to enable the researcher to get to know their animals, and thereby specify clearly what is to be explained.

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