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Review

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Taking note of Tinbergen, or: the promise of a biology of behaviour

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In this concluding paper, we revisit Tinbergen's 1963 article and assess its impact on the field of behavioural research in general, and the papers in this volume in particular. We show how Tinbergen's insistence that greater attention should be paid to studies of 'survival value' has yielded immense returns over the past 50 years, allowing an integrative biology of behaviour to emerge and thrive, and that his addition of ontogeny to the 'major problems of biology' was both insightful and prescient.

> Huxley likes to speak of 'the three major problems of biology': that of causation, that of survival value and that of evolution—to which I should like to add a fourth, that of ontogeny.
> Tinbergen [1, p. 411].

1. The value of survival value

There are very few behavioural researchers, if indeed any, who remain ignorant of Tinbergen's seminal paper [1], with its message that we should ask questions at the different levels of analysis corresponding to the 'major problems in biology'. It is nevertheless interesting to re-read the paper, and be reminded that it was Huxley who first identified the 'major problems of biology' in this way (with, no doubt, a nod to Aristotle along the way), and that Tinbergen's contribution was the idea that we should add ontogeny to the problems of causation, survival value and evolution [1]. Even more interesting from our perspective is that a large proportion of the paper is given over to a plea for more studies on 'survival value'; that is, the ultimate, functional explanations for why animals do what they do. Indeed, it is by far the longest section of the paper, and also the most polemical. It seems odd to think that Tinbergen had to mount a defence of this approach, and insist on its importance when, today, behavioural ecology dominates the study of animal behaviour, and has, until very recently, focused almost exclusively on studies of survival value. It also gives an interesting twist to any assessment of Tinbergen's influence with respect to the study of behaviour. On the one hand, it could be argued (as we do in our introduction) that integrating all of Tinbergen's questions in a single research programme is an ideal that is rarely achieved and that, as such, we have failed to implement the project that Tinbergen laid out for us. On the other hand, one could equally well argue that, by building up an extensive, extremely comprehensive, body of knowledge on the ultimate function of many and varied behaviours, among a wide variety of species [2], we have, in fact, followed his advice to the letter. Having done so, it is also true to say that we are now in a better position to integrate the different levels of explanation in a truly satisfactory way. The reason for this is twofold.

First, behavioural ecological studies have successfully identified the adaptive strategies displayed among many and varied taxa, and they have achieved this

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by using the simplifying assumption of the phenotypic gambit [3]: the idea that natural selection will find a way to produce adaptive behaviour unconstrained by genetic or physiological mechanisms (the assumption of no psychological constraints has recently been termed the 'behavioural gambit' by Fawcett *et al.* [4]). In other words, a great deal of behavioural ecology's success came about by explicitly ignoring the other levels of explanation advanced by Tinbergen and Huxley before him.

With respect to the ideas presented in this volume specifically, one could argue, as Thierry [5] does, that the heuristic value of the 'synthetic socioecological model' of primate social organization, first put forward by van Schaik [6], lies precisely in its status as a 'null model' in which ecological factors alone are considered as determinants of social structure. As with all good heuristic devices, it has proved to be self-limiting: by spawning a series of field studies aimed at testing the model, many of which failed to support its predictions, we have not only gained insight into the kinds of data still needed to answer questions at the functional level, as Koenig *et al.* [7] point out, but also, as Thierry [5], Kamilar & Cooper [8] and Holekamp *et al.* [9] note, we can now recognize the degree to which observed behaviour reflects constraints on available genetic variation and developmental processes; processes that are themselves the result of the constraining influence of particular historical evolutionary events. In other words, the starting assumption of no behavioural constraint—our notion of a 'Tinbergian demon' [10]—is precisely what enables us to recognize when constraints are, in fact, operating. In this way, the greater attention given to survival value in the 50 years since Tinbergen wrote his paper has ineluctably led us into a more detailed consideration of other levels of explanation, and the role of constraint in behavioural evolution. As Holekamp *et al.* [9] remind us, behaviour is not necessarily more developmentally plastic than morphological or life-history traits, and can be constrained in much the same way (which echoes rather nicely Tinbergen's [1] point that behavioural patterns can be considered as 'organs').

More specifically, as Thierry [5] points out, phylogenetic history cannot be ignored when considering patterns of interspecific variation. His studies of macaques have shown how different personality traits tend to cluster in stable combinations within and across the different species in ways that are resistant to local ecological influence [5]. An approach that ignores evolutionary history similarly fails at the intraspecific level: rates of infanticide, male mating strategies and patterns of coalition formation are similarly resistant to explanation by local ecological factors among the *Papio* baboons [11]. Historical influences of this nature may partly explain why, as Koenig *et al.*'s [7] review indicates, ecological factors do not predict aspects of primate sociality with any great accuracy; a finding that stands in contrast to Faulkes & Bennett's [12] analysis of mole-rat sociality, where a single ecological factor, aridity, reveals itself to be a very strong predictor of social organization. Populations of long-lived species such as primates may experience more historical accidents (with respect to, e.g. climate) resulting in behavioural responses that are unpredictable from the point of view of a socioecological model that assumes animals are responding only to current local ecology. Such species may also rely more heavily on forms of social learning that, as Cantor & Whitehead [13] detail in their analysis of cetacean societies, result in feedback loops between behavioural strategies and social structure that again give rise to more complicated evolutionary dynamics than are captured by existing socioecological models.

Another reason why current socioecological models often fail is perhaps due to their emphasis on entities above the individual level, such as dominance style [6]. Such a stance contains the implicit assumption that such patterns arise because all individuals respond in a uniform fashion to their ecological and social circumstances. As Montiglio *et al.* [14] point out, however, work on animal personality and individual differences suggests that the coevolution of habitat-specific performance and habitat preference could lead to the evolution of multiple, locally adapted specialists. Applied to the social domain, this suggests that individuals may select certain situations or be prepared to engage in certain kinds of interaction, and avoid others, depending on their particular suite of linked behavioural traits. Bringing this idea to the socioecological model, it seems likely that social groups will be composed of individuals with varying dispositions (as a result of particular kinds of gene–environment interactions, as demonstrated by Runcie *et al.* [15] or various kinds of epigenetic effects: see below), such that the social system is an emergent property of these dynamic social interactions rather than a monolithic entity, a point also argued by Blumstein [16] in his study of marmot social systems. Montiglio *et al.*'s [14] analysis thus suggests that, if we investigate immediate ontogenetic history and its influence on proximate mechanism, as well as patterns of phylogenetic history, as suggested by Thierry [5], we could begin to identify a series of tractable, well-specified problems that could be tackled in a series of formal models (see [17] for some examples of problems that the current socioecological model cannot explain), rather than continue to assume that simple (verbal) models can capture the complexity that clearly exists. In this way, we may be able to generate the means by which we can link individual-level processes to group-level and population phenomena [18,19], and to evolutionary change over time. The broader point to make here, then, is that Tinbergen's [1] hopes for integration are now being realized at least partly because we have heeded his plea for a stronger focus on functional explanation; a strongly functional perspective directs our attention to the possibility that mechanistic diversity may itself often be adaptive [20]. Understanding the manner in which such diversity is produced and maintained, and how this works both phylogenetically and ontogenetically is clearly another avenue we can now pursue more effectively thanks to our greater understanding of adaptive function, linking to work at the molecular genetic level on the 'evolution of evolvability' [21].

The second reason why we are now poised to adopt an integrative approach to mammalian behaviour reflects the release of constraints on our ability to conduct the kinds of research needed. Innovations and improvements in techniques and methods over the last 50 years (ranging from more field-friendly, non-invasive techniques to monitor physiological processes, to improved molecular and genetic techniques that permit the study of gene–environment interactions, as well as epigenetic and epistatic effects, to the increased computing power that has enabled more powerful forms of statistical and phylogenetic analyses) have allowed us to conduct more sophisticated, wide-ranging studies that naturally combine two or more levels of explanation. Indeed, all the papers in this volume are testament to this greater capacity and willingness to exploit new methodological and analytical techniques, in both the laboratory and the field. It is also true that many of the papers here vindicate Tinbergen's [1] strongly held views concerning the value of naturalistic description and observation, another of the 'bees in his bonnet' (p. 430): it is clear that long-term field studies of particular taxa have been instrumental to the identification of relevant questions at all levels of analysis [22], and that intraspecies comparisons are crucial to characterizing both flexibility in social structure and social behaviour, so leaving behind the constraining influence of typological and essentialist thinking.

2. The addition of ontogeny

Perhaps the most striking aspect of Tinbergen's paper, however, is the degree to which his addition of ontogeny as one of the 'major problems of biology' has been borne out by current scientific developments, notably the rise of evolutionary developmental biology, so-called 'Evo–devo' ([23–25] but see [26] for a critique). There has been a breakdown of the classic distinction between 'vehicles' and 'replicators', stemming from the recognition that DNA is not the sole controller of molecular mechanisms, but is instead just one part of a complex nexus of interacting processes that the cell uses during development; genes operate in constant cycles of interaction with each other, and with the environment (cellular, physical and social) in which they are embedded, and they do so throughout the lifespan of the individuals, as regulatory networks respond to changes in an individual organism's circumstances [23–25,27]. This shift in our understanding of the ways in which cellular and genomic processes interact, and the rise of epigenetics [28], has forced a greater acknowledgement of the fact that natural selection acts over the entire life cycle of an organism: aspects of the adult phenotype may be tied to specific aspects of development that trade-off against each other, and it is clear that epigenetic influences in early life can influence the subsequent life course in far-reaching ways [29]. As noted above, technological and methodological innovations are in large part responsible for presenting these new opportunities, and behavioural researchers have been swift to apply these techniques and reap the benefits. Consequently, it is becoming increasingly clear that, as Holekamp *et al.* [9] note, a developmental perspective helps to bridge the gap between proximate and ultimate explanations—the traditional focus of behavioural researchers—because it draws our attention to the origins and adaptive value of behavioural variation, so enabling a better understanding of the range of phenotypes available to selection. By the same token, the addition of ontogeny naturally brings in the phylogenetic level of explanation; we are beginning to appreciate more fully how significant evolutionary change may be brought about by small changes in gene regulatory mechanisms, and the manner in which these cascade throughout development to produce large changes in the phenotypic characteristics that are visible to selection [30].

Both Sachser *et al.* [29] and Holekamp *et al.* [9] demonstrate the influence of social factors with respect to epigenetic effects, exemplifying this integrative approach, and illustrating its scope: guinea pigs and hyaenas are very different kinds of creatures, but social influences—most notably those of mothers—produce long-lasting effects on offspring development and behavioural responses as adults; their studies highlight how particular kinds of social stressors can produce adaptive developmental plasticity with respect to prevailing or future environmental conditions. In addition, Sachser *et al.*'s [29] finding that these effects are a feature of adolescence and not simply the pre- and early post-natal periods shows how adaptive adjustment can be quite finely tuned. In similar fashion, Faulkes & Bennett [12] trace the neurobiological and developmental underpinnings of the mole-rat adaptation to arid environments and, like Sachser *et al.* [29] and Holekamp *et al.* [9], provide an exemplary case study of the value of a fully integrative approach. Runcie *et al.* [15] add to this by showing how an integrative, developmentally oriented approach can help explain individual differences in baboon behaviour, via an exploration of gene × environment interactions (GEIs). Much like Sachser *et al.* [29], Runcie *et al.*'s [15] findings reveal an effect of the social environment on gene expression that extends beyond the early developmental environment, reinforcing the notion that adaptive adjustments can be made throughout the lifespan, as well as demonstrating that GEIs are dynamic processes, rather than fixed traits. Thus, while developmental processes can be viewed as constraining influences on behavioural expression, it is clear that these constraints are instrumental to generating flexibility in the adult organism (regardless of whether that flexibility is adaptive). This is worth noting because we tend to view constraint and flexibility as antithetical, or as the opposing poles of a continuum, but the integrative work presented here suggests that we should perhaps consider them, not as opposites, but as complementary, as two sides of the same coin [31].

The role of the social environment in shaping genetic reaction norms also has obvious links to Montiglio *et al.*'s [14] suggestion that assessments of indirect genetic effects are needed to probe the degree to which an individual's behaviour can be considered an inherent characteristic or a response to the particular range of conspecifics encountered. Blumstein's [16] findings that certain network characteristics of marmots show a high degree of heritability, most notably the tendency of certain individuals to receive aggression from others, demonstrates the value of this approach and again highlights the way in which the incorporation of new techniques—in this case, social network analysis with quantitative genetics—can allow us to answer relevant evolutionary questions in greater depth, under natural conditions [20,32]. It is also worth noting again that long-term studies of mammals are particularly well suited to such analyses [22], allowing us to gain novel, integrative insights, and we can expect to see more such studies in the future.

3. Social flexibility versus flexibility in social behaviour

One very useful distinction made in this volume is Schradin's [33] notion of 'social flexibility' versus 'flexibility in social behaviour'. Social flexibility refers to reversible changes in social and mating tactics at a population level, whereas flexibility in social behaviour refers to individual variability in response to changing circumstances. Schradin's study species, the African striped mouse, epitomizes a socially flexible species that can be found in solitary, single family and extended family groups [33]. His argument is that, lacking an ability to adjust individual social behaviour in response to increased conflict between group members, striped mice switch their patterns of social organization moving from group to solitary living and back again, as circumstances dictate. Ecological constraints that produce changes in population density and demography serve as the triggers for these shifts in the short-term, and the level of unpredictability in the environment comprises an important selective force for the evolution of social flexibility. In addition to Schradin's [33] work on striped mice, Blumstein [16] also describes how, in yellow-bellied marmots, an increase in population density gave rise to a higher proportion of multi-male groups, but this did not, in turn, result in an increase in cooperative behaviour (coalition formation) between males; thus, marmots also appear to be socially flexible, but do not show flexibility in social behaviour.

In contrast, primate species show little social flexibility—indeed, they show a marked conservatism with respect to their social organization (composition of groups)—but are highly flexible with respect to their individual social behaviour. As Schradin [33] argues, it is probably this flexibility at the individual level that allows them to maintain their species-specific social organization in a 'homeostatic' fashion (see also [34,35]). Henzi *et al.*'s [36] inter-population comparison of vervet monkeys illustrates this point perfectly: increased group size has scalar effects on social structure (i.e. the way in which animals interact with each other) producing marked differences in patterns of grooming and agonistic behaviour across populations, but in the context of identical patterns of multi-male multi-female social organization (see also [37] for similar reports of demographic effects on behaviour). As such, it provides a link to Runcie *et al.*'s [15] analysis, where group size was found to be a strong predictor of GEIs influencing gene expression. In line with this, Kamilar & Cooper [8] show that, while many aspects of social systems among the primates show a significant phylogenetic signal, these are generally lower than a Brownian motion expectation, suggesting a degree of behavioural plasticity among the primates.

Van Schaik [38] makes essentially the same argument as Schradin [34], but approaches the issue from the primate perspective, with an emphasis on brain size evolution. His argument is that flexibility in behaviour is limited by brain size, hence organisms that are small, face high predation, live in seasonal environments or lack opportunities for social learning cannot evolve greater flexibility in behaviour, as large brain size is not favoured by selection. Instead, smaller brained species must achieve local adaptation through selection on specific genotypes (although, as Schradin [34] points out, the story may be more complex; developmental plasticity and epigenetic effects could also produce locally adaptive responses, as Sachser *et al.*'s [29] work demonstrates). As animals' brain and body size increase, adaptation to local circumstance is more frequently achieved by selection on behavioural flexibility and, because of their greater mobility and longevity, these species also have greater need for such plasticity. Data from orang-utans supports this idea, but also indicates that there can be significant costs: high flexibility buffers apes against environmental change, but also means that these animals respond very slowly to selection because of the constraints introduced by long generation times and slow reproductive turnover; these traits are likely to be strongly detrimental under conditions of drastic environmental change, such as anthropogenic habitat destruction. One can also make a link between van Schaik's [38] argument and Holekamp *et al.*'s [9] discussion of the morphological constraints that limit the extent to which the carnivores can undergo brain expansion. Carnivore jaws and skulls are built to resist high stresses and exert strong bite forces. Any expansion in brain volume thus impinges on available muscle area within the zygomatic arches, and reduces the maximal bite force possible. Holekamp *et al.* [9] argue that, in the trade-off between brain size and bite force, the balance has been tipped in favour of the feeding apparatus. The lack of equivalent behavioural flexibility in carnivores as compared with primates, despite often striking similarities in social organization and structure (as is the case for the spotted hyaena) thus supports van Schaik's [38] suggestion that flexibility in social behaviour is ultimately limited by the degree to which brain size expansion is possible within a given lineage.

Holekamp *et al.* [9] argue that other morphological constraints among carnivores may also limit the evolution of behavioural flexibility. Specifically, they argue that the locomotor necessity for paws, rather than hands, has a strong influence on the kinds of social engagement possible in comparison to primates, and perhaps also limits the evolution of cultural behaviours (many of which involve the manipulation and modification of physical objects). As Cantor & Whitehead [13] show, however, such constraints do not necessarily prevent cultural evolution from occurring. Cetaceans also lack hands, but show distinct vocal traditions that are socially transmitted and shared within distinct subsets of the population, thus satisfying the definition of culture [13]. Indeed, it seems more likely that the limits on carnivore culture arise owing to another constraint pointed out by Holekamp *et al.* [9], namely, the lack of opportunity for offspring to learn socially from their mothers as a consequence of denning. This is something that Cantor & Whitehead [13] also consider more broadly, when they highlight the links between social structure, social learning and the transmission of cultural traits and, incidentally, once again bring home Tinbergen's [1] point about the value of description and observation: it is apparent that we need better and more detailed descriptions of social structure (including the valuable quantitative insights provided by network analysis [13]), and preferably over the long-term [22], if we are to fully understand the nature of the feedback between social structure and socially acquired/transmitted behaviours.

4. Conclusion

To conclude our paper, and this special issue, we turn to Tinbergen's [1] own conclusion. Here, he reiterates his intent to pay tribute to Konrad Lorenz as 'the father of modern ethology' and emphasizes that he has been 'at pains to develop . . . the thesis that we are witnessing the fusing of many sciences, all concerned with one or another aspect of behaviour into one coherent science, for which the only correct name is 'Biology of Behaviour' (p. 430) and that what really mattered was 'the growing awareness of the fundamental unity' (p. 431) of this endeavour. The papers in this volume suggest that Tinbergen's thesis has been proven and the promise of a unified Biology of Behaviour is now coming to fruition. He would, we think, be pleased.

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