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## Introduction

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# Constraints and flexibility in mammalian social behaviour: introduction and synthesis

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This paper introduces a Theme Issue presenting the latest developments in research on the interplay between flexibility and constraint in social behaviour, using comparative datasets, long-term field studies and experimental data from both field and laboratory studies of mammals. We first explain our focus on mammals and outline the main components of their social systems, focusing on variation within- and among-species in numerous aspects of social organization, mating system and social structure. We then review the current state of primarily ultimate explanations of this diversity in social behaviour. We approach the question of how and why the balance between behavioural flexibility and continuity is achieved by discussing the genetic, developmental, ecological and social constraints on hypothetically unlimited behavioural flexibility. We introduce the other contributions to this Theme Issue against this background and conclude that constraints are often crucial to the evolution and expression of behavioural flexibility. In exploring these issues, the enduring relevance of Tinbergen's seminal paper 'On aims and methods in ethology', with its advocacy of an integrative, four-pronged approach to studying behaviour becomes apparent: an exceptionally fitting tribute on the 50th anniversary of its publication.

## 1. Introduction

Behaviour is one of the key interfaces between an animal and its environment. Animals must act to gain access to food and other vital resources; to find suitable habitats; to maintain homeostasis; to avoid becoming food for others; to find and select mates; to rear their offspring successfully and to manage their social relationships with conspecifics. Behaviour therefore represents a major mechanism influencing an individual's inclusive fitness, and thus ultimately evolutionary change [1,2]. Adaptive behavioural solutions to recurrent, predictable environmental and social problems should therefore be favoured by selection, resulting in robust, species-specific behaviour patterns [3]. Thus, optimal behavioural rules can evolve [4], leading to an intraspecific reduction in behavioural options. While there are several other main constraints on the evolution of behaviour (see §4), this particular one is central to understanding behavioural adaptations. Its importance derives from the fact that animals typically first respond behaviourally to changes and challenges in their environment, whereas adaptations of their morphology, physiology and life history take much longer [5]; indeed, tests of an influential concept in behavioural ecology demonstrated that mobile animals respond quickly, often in an ideal-free manner, to variation in resources, predators and competitors [6]. In fact, maximal behavioural flexibility might be generally advantageous in various natural situations [7,8], including adaptations to climate change [9]. Thus, as has long

been recognized [10,11], evolution also places a premium on behavioural plasticity or flexibility, creating an apparent dilemma for behavioural adaptation. Understanding the scope and limits of behavioural flexibility is therefore critical to understanding organismal adaptation. This is especially true when our aim is to understand the inherently dynamic nature of social behaviour, which by definition, concerns interactions among two or more individuals with potentially diverging interests.

With this Theme Issue, we contribute to the conceptual integration required for a deeper understanding of the processes that enable and constrain behavioural flexibility in a social context. Such an endeavour is best served by an integrative approach that draws on Tinbergen's [12] seminal insights that the evolution of a behaviour pattern cannot be seen in isolation from the underlying neuronal and hormonal mechanisms that give rise to it, as well as the genetic and environmental factors directing relevant developmental processes and the adaptations of ancestral species that underlie current adaptations. While Tinbergen was well aware of the fact that certain constraints can 'stabilize' the behaviour of a species, in his 1963 paper he discussed the fact that causal and motivational mechanisms constrain the path of evolution only in passing. Given the practical constraints related to the increasing specialization of students of animal behaviour today, the four approaches outlined by Tinbergen have rarely been applied to a particular problem in the same species. By emphasizing the value and necessity of applying such an integrative approach to the study of flexibility in social behaviour, we hope to inspire behavioural and evolutionary biologists to adopt this more integrative perspective themselves [13] and also encourage more dialogue between field and laboratory scientists. The 50th anniversary of Tinbergen's influential publication provides a timely occasion for such encouragement, thanks to the recent methodological progress in genetics, developmental biology, neurobiology and molecular physiology that have made it possible to identify the interdependencies between ultimate and proximate determinants of behaviour in unprecedented detail, as well as a juncture to also acknowledging the influence of Julian Huxley, D'Arcy Thompson and others on Tinbergen's thinking [14].

To facilitate these goals, this introductory paper first outlines the relevant aspects of social behaviour, its determinants and corresponding mechanisms. We then characterize the complementary processes and mechanisms that both constrain behavioural responses and generate flexibility (for a more general perspective, see [15]), integrating the main questions addressed by the other contributions to this Theme Issue into this discussion.

## 2. Social behaviour

It is clear that behaviour is an important pacemaker of evolutionary change, either by exposing animals to new selection pressures or allowing them to evade such pressures in contexts that have direct consequences for survival or reproduction. Here, we wish to focus specifically on patterns of social behaviour, i.e. those that involve effects on or by conspecifics, in most cases mediated by communication or direct interaction. The comparative study of social behaviour has sometimes been hampered, however, by a failure to

adequately define the variables of interest, with respect to both behaviour itself and the social context in which it occurs; that is, with respect to the structure of the social system. In what follows, we first elaborate briefly on why our approach is focused on mammals and then define the three components of their social systems.

### (a) Mammalian social behaviour

Mammals are an excellent taxon in which to investigate constraints and flexibility in social behaviour because they show an extremely broad range of social systems, along with equivalent variation in social complexity, behavioural flexibility, brain size and cognitive abilities [16–19]. Compared with other taxa whose social behaviour has been well studied, notably birds and social insects, mammals exhibit more inter-specific variation in the pace of development (which affects time available for learning), length of the lifespan (which influences options to establish and manage multiple, long-term individualized social relationships in complex networks) and finally, brain size (which modulates behavioural decisions through variable cognitive abilities).

Social behaviour of other taxa is, of course, also characterized by complexity and sophistication; in fact, there is substantial evidence to suggest that the same principles discussed in this Theme Issue are also important determinants of the social behaviour of non-mammalian taxa. To cite just a few examples, some bird species can live or be kept in either pairs or flocks [20], whereas others are strictly pair-living and intolerant of intruders [21], indicating convergent patterns across birds and mammals (see below). Similarly, monogamous mating has been identified as a phylogenetically robust condition for the evolution of cooperative breeding in social insects [22], birds [23] and mammals alike [24]. As in mammals, aspects of the social system of other taxa also exhibit distinct patterns of variation above the species level, such as cognitive abilities [25,26] or patterns of parental care among birds [27]. Finally, individual animals in numerous invertebrates and vertebrates have been shown to differ in their average level of behaviour displayed across a range of contexts, and in their responsiveness to environmental variation, suggesting similar underlying mechanisms [28]. We do not, therefore, advocate any sort of mammalian supremacy; instead, our emphasis on mammals is solely motivated by the hope of achieving a sharper focus on the key issues we wish to consider by controlling for fundamental life-history traits and constraints, such as internal gestation and lactation, that are known to affect behaviour.

### (b) Components of social systems

Social systems can be decomposed into three interrelated, but heuristically distinct, components. First, *social organization* is defined as the size, composition, cohesion and genetic structure of a social unit [29]. Three fundamental types of social organization can be distinguished: adult individuals can either lead solitary lives, coordinate their activities with a member of the opposite sex by forming pairs, or they associate and coordinate their activities with two or more conspecifics by forming groups. Most variation in social organization occurs among-species, but it is interesting to ask why some species are apparently invariable in this respect, whereas others exhibit intraspecific variation and flexibility (either among populations or even among social units within local

populations) in these traits. For example, some species can be found or housed in either pairs or groups [30,31], whereas others are intolerant to adding individuals to pairs [32], or to changes in the composition of their group [33].

Second, we consider the *mating system* as a distinct, functionally important subset of interactions that describe who mates with whom (and how often). Depending on the average number of mating partners of males and females, monogamous, polygynous, polyandrous and promiscuous mating patterns can be discerned [34]. A particular mating system represents the outcome of the combination of sex-specific reproductive strategies and the resolution of an underlying sexual conflict. Because of variation in the operational sex ratio, age- or condition-dependent mating preferences and other factors, individual mating decisions tend to be flexible both among individuals and across time, but they may also be strongly constrained by aspects of social organization or dominance. For example, in groups of wolves, meerkats and tamarins, only one adult female will typically reproduce, even though several are present [35]. The extent to which matings can be monopolized by dominants (of either sex), i.e. the degree of reproductive skew, is also influenced by several factors, including group size and kinship, so that the outcome varies not only among, but also within-species [36,37].

Third, *social structure* is defined as the sum of all social relationships. Each dyadic social relationship is defined by the quality and patterning of interactions (except matings) between its members [38]. How an individual interacts with a particular conspecific depends on numerous factors, including age, sex, kinship, dominance, personality and condition. We therefore expect to see behavioural plasticity across an individual's lifetime, but also substantial variation between individuals, among social units within a population [39,40] and among populations inhabiting ecologically different habitats [41]. Despite this variation, however, it is also true that other aspects of social structure, such as the steepness of dominance gradients or tolerance levels, are highly invariant and can be used to characterize the dominance style of a given species [42]. Thus, much social behaviour can be studied from the perspective of flexibility and constraints on action, and we turn next to a consideration of their biological bases.

### 3. Determinants of behaviour

To consider all determinants of behaviour, an integrative research agenda that addresses all four of Tinbergen's questions concerning mechanism, development, function and phylogeny is required. Given various practical and ethical constraints, however, a comprehensive Tinbergian approach is rarely seen in the studies of a single mammalian society. Indeed, classical ethologists were initially (and still are) mainly interested in mechanism and development [43], whereas behavioural ecologists have tended to focus on the function of social behaviour [44]. Moreover, studies of the determinants of individual behavioural variation have been largely isolated from efforts to illuminate reproductive strategies or patterns of social structure and vice versa. Only recently have research agendas included conceptual and empirical attempts to generate integration across hierarchical and functional levels of behavioural variation, for example, in the studies focusing on alternative reproductive tactics [45], kin selection [46] and animal personalities [47].

The insights gained from truly integrative studies may be profound [13,48].

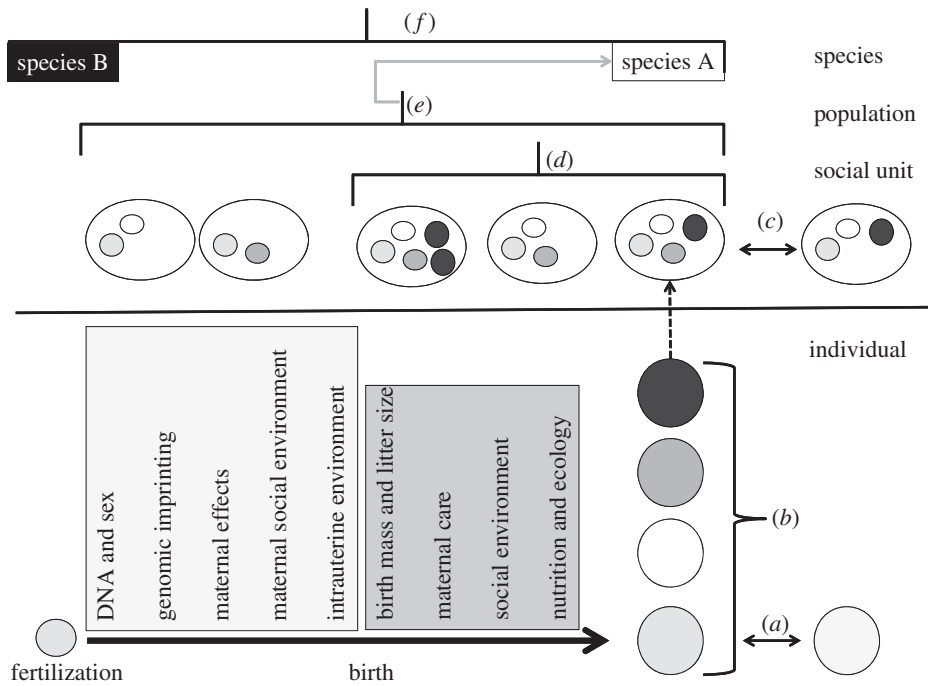
#### (a) Levels of variation

Behavioural variation exists among individuals, social units (local neighbourhoods of solitary individuals, pairs or groups) and among populations owing to different factors and processes (figure 1). Sources of variation in individual behaviour, which form the basis for variation in social structure, have been mainly characterized by studies of mechanisms and development [49]. At fertilization, the unique genetic make-up of an individual is determined by combining parental sequences of DNA, some of which have a function in shaping behavioural patterns after birth. In mammals, the sex of an individual, which later on explains much individual behavioural variation, is also chromosomally determined at this point. During foetal development, genomic imprinting, i.e. the fact that certain genes are expressed in a parent-of-origin-dependent manner [50], may have lasting effects on the development and later behaviour of siblings [51]. Other epigenetic processes that involve modification of DNA sequences that serve to modulate gene expression during pre- or post-natal development can also lead to predictable behavioural outcomes later in life [52]. Maternal effects as a result of differential maternal provisioning of eggs with hormones or mRNAs can affect individual development and post-natal behaviour [53,54]. Social experiences by the mother, such as stress, can have long-lasting, sex-specific effects on the behaviour of her offspring, leading to masculinization of daughters and infantilization of sons [55]. Similar effects can be evoked by variation in intrauterine position and litter sex ratio [56,57].

In addition to individual learning, important post-natal factors known to affect variation in individual behaviour include birth mass [58], litter size [59], maternal care [60], nutrition [61], and the subsequent physical and social [62] environment. Most of these insights on determinants of individual variation in social behaviour are based on studies of laboratory rodents, providing a basis for future validation under naturalistic conditions and in other taxa.

Research has also addressed the causes of behavioural variation among social units within populations, within social units over time and between populations within-species [63]. Intraspecific variation in social systems has been attributed to (chance) demographic effects, environmental change, social context or local culture. In several species of callitrichid and lemurid primates, for example, neighbouring social units may consist of pairs, one female and several males, one male and several females or multiple males and multiple females, respectively [64–67]. In addition, individual groups may exhibit any or all of these types of social organization over time. This variation is presumably due to variation in stochastic demographic events in small groups [68], whereas interannual shifts between solitary- and group-living in striped mice (*Rhabdomys pumilio*) depend on population density and resource abundance [31]. In gorillas (*Gorilla gorilla*) and in some langurs (*Presbytis* spp.), predictable variation in the number of males per group is related to varying risks of infanticide [69,70].

Local variation in social behaviour among groups is mostly due to differential innovation and subsequent social transmission. White-faced capuchin monkeys (*Cebus capucinus*),



**Figure 1.** Determinants of behavioural flexibility. Determinants and levels of behavioural flexibility are depicted for individuals (below solid line) and social units (above solid line). Beginning with fertilization (lower left corner), several factors shape individual behaviour patterns, both before (light grey box) and after birth (dark grey box). (a) Over their lifetime, individuals may exhibit social flexibility (or ‘plasticity’) in particular behaviour patterns. (b) Different individuals of the same species may exhibit interindividual variation in behaviour (‘personality’). (c) Individuals are socially organized into social units (neighbourhoods, pairs or groups) that may exhibit variation in social organization over time or (d) within populations (d), either as a result of chance effects or changes in environmental conditions. Behavioural variation at this level is mostly due to transmission of socially learned behaviour patterns. (e) Different populations of the same species may vary in social organization, mating system or social structure, presumably most often in response to ecological gradients. (f) Species differences in social systems appear to have a strong genetic component, including phylogenetic signals.

for example, exhibit a rich repertoire of group-specific social conventions that appear to serve solely to test social bonds [71]. Across mammals, there is similar group-specific variation in specialized foraging techniques [72,73], tool use [74,75] and communication signals [76,77]. Much of this variation is transient, however, unless there are strong social or ecological pressures maintaining particular behavioural styles [78]. Finally, with increasing geographical distance among sub-populations, ecological factors are more likely to vary in ways that influence behavioural variation among populations. These factors include population density [79], predation risk [80,81] and food availability [82].

## (b) Variation in social system components

To study flexibility in social behaviour, we need a clear idea about the components of social systems exhibiting inter- and intra-individual variation and of the factors known to cause it. This section therefore summarizes variation in mammalian social organization, mating systems and social structure along with the relevant theoretical underpinnings, reflecting the primary occupation of behavioural ecologists with these topics.

### (i) Social organization

Intraspecific variation in social organization in mammals and other vertebrates is widespread. Any combination of solitary-, pair- and group-living is theoretically possible within a species, but co-occurrence of all three types, i.e. an effective lack of modal social organization has been reported only for some species of rodents [83–85]. Further, pair-living should be rare or unstable when other options are available because male reproductive

potential is most constrained in this situation [86]. Phylogenetic reconstructions of different types of social organization can reveal which evolutionary transitions were most common, thereby generating predictions about the likelihood of co-occurrence of different types of social organization among living taxa. In primate evolution, for example, most transitions occurred between solitary and group-living taxa, and between group- and pair-living ones [87], respectively, predicting that the co-occurrence of solitary individuals and pairs in the same species should be rare. Strong signals in the reconstruction of evolutionary transitions to cooperative and communal breeding in mammals [24] may similarly predict intraspecific variation between cooperative breeding and pair-living, and between communal breeding and groups with plural breeding and polygyny in some contemporary species. The co-occurrence of groups and solitary individuals may reflect an unstable balance between the ecological and social factors generating costs and benefits of living in groups [88], with variation in predation risk and food abundance being the most important factors [85,89–92]. Intraspecific variation between groups and pairs [93], or between groups with one or multiple males [94–96], can be largely attributed to the outcome of sexual conflict over sex-specific reproductive strategies [97–100].

### (ii) Mating system

A large body of theory has been developed and tested by behavioural ecologists to explain interspecific variation in mating systems. Briefly, because sex differences in potential reproductive rates are particularly pronounced in mammals, males are assumed to maximize their reproductive success by increasing mating opportunities, whereas female

reproductive success is more strongly dependent on sufficient access to resources [86,101,102]. Resource distribution and quality, together with predation risk, are therefore the main determinants of female distribution [103], and males then go where the females are [104] and try to monopolize as many of them as possible (which further depends on the temporal distribution of their receptive periods) [100]. If single females are widely spaced out, then individual males will either try to defend access to one (monogamy) or several (polygyny or promiscuity) of them. In cases where females form groups, they are either joined (permanently or only during the breeding season) by one (polygyny) or multiple (promiscuity) males. Polyandry is unexpected among mammals for the reasons mentioned earlier, and because female philopatry is common in mammals, it is, indeed, the rarest form of mating system [34,105].

For species in which several females and/or males reproduce, a large body of theory has been developed to explain how reproduction is partitioned among same-sex group members. Two main classes of reproductive skew models have been proposed, each making different assumptions about the underlying mechanisms and key factors [106]. Briefly, according to transactional models, reproductive skew is the outcome of reproductive transactions between dominant and subordinate group members, mediated either by the subordinates' threat to leave the group (concession-based models) or by the dominant's threat to evict them (restraint model). By contrast, compromise models assume that reproductive skew is the outcome of a struggle over reproduction between group members, the intensity of which is mediated only by the detrimental effects it imposes on group productivity. Most studies of reproductive skew in mammalian societies have found support for compromise models or a less formalized class of models that focus on priority-of-access [35–37] (but see [107,108]).

### (iii) Social structure

Two bodies of theories exist to explain variation in social structure. The socioecological model is a verbal model that predicts species differences in female social relationships in group-living species as a function of variation in resource distribution and quality [109]. Under different combinations of resource clumping and distribution, four major types of competitive regimes are favoured that reflect different intensities of within- and between-group competition [110]. Because cooperative defence of resources is sometimes possible, patterns of female dispersal and the resulting genetic relationships also play a role in this model. In some taxa, for example in macaques, competitive regimes can also be predicted from phylogenetic relationships, indicating the presence of phylogenetic effects [111]. This model mainly speaks to primate data [112], but it has been used to study interspecific variation in female social relationships in other taxa as well [113]. However, it fails to provide complete explanations for many social phenomena among primates and other mammals [114], partly because of a strong focus on ecological factors alone.

Kin selection theory provides a framework for studying patterns of cooperative behaviour especially among females, because most mammals are characterized by female philopatry and relatives live together, or at least in close vicinity [17,115]. Mutualism and manipulation can also explain

some examples of cooperative behaviour, especially among non-kin [116]. Recent work has emphasized the fact that relatives also compete with each other, so that social relationships among relatives are more complex and diverse than simple kin selection models may suggest [117,118]. For social relationships among males and for those between the sexes, no explicit theoretical models exist; they are assumed to be largely influenced by sex-specific reproductive strategies [119,120], including infanticide [121,122], and counter-strategies.

## 4. Constraints and flexibility

The concept of a 'Darwinian demon', a hypothetical organism that starts reproduction at birth and produces copious numbers of offspring forever after [123], has played an important role in advancing life-history theory by identifying constraints and trade-offs in the real world [124]. There may therefore be equivalent heuristic value to thinking of a 'Tinbergenian demon', i.e. a hypothetical organism that, after fertilization, has unlimited opportunities to acquire and exhibit any behaviour pattern during the course of its lifetime. A similar notion has been recently discussed as the behavioural gambit, i.e. the assumption that psychological mechanisms do not constrain the development and expression of adaptive behaviour patterns that allow animals to reach the optimal solution to a given problem [3]. Such null models might be useful by prompting us to identify those factors and mechanisms that may influence the behaviour of real animals, thereby contributing to a more integrative understanding of the determinants of behaviour and their interactions, for example, through reciprocal causation [125], as well as of the potential costs of flexibility [126].

Tinbergenian demons do not exist because some, if not most, theoretically possible behavioural options are constrained as a result of the operation of at least four broad classes of pressures and constraints. Before summarizing these, it is useful to be clear and explicit about the nature of constraints [127], types of flexibility [128] and the levels at which they are observed [28,129,130]. We should note, however, that a separate discussion of them is justified only by reasons of clarity; the mechanisms underlying these constraints are so inextricably linked that, in reality, it is not possible to make this clean separation [125].

### (a) Genetic constraints

One fundamental set of constraints is related to the genetic basis of species-specific traits that have evolved and differentiated during recursive rounds of adaptation and speciation over millennia, underpinning advantageous patterns of robustness that may turn into constraints under changing conditions (see also van Schaik [131]). The developmental trajectories of a recently fertilized oocyte of, say an insect, a fish or a mammal differ substantially from each other because of their divergent genetic make-up. While these genetic differences generate a number of 'trivial' constraints on behaviour, such as the inability of elephants to fly or that of insects to lactate, the genetic underpinnings of successful species-specific behavioural solutions to recurrent, predictable challenges to survival and reproduction will automatically eliminate many other potential behavioural solutions to the same adaptive problems, thereby explaining some species differences in behaviour.

For example, genetically determined, species-specific patterns of oxytocin and vasopressin receptor distributions in the forebrain in closely related species of voles (*Microtus* spp.) are linked either to a monogamous or promiscuous mating system with their attendant behavioural consequences [132], reflecting constraints on development in existing species. Similarly, van Schaik [131] argues that species differences in brain size in orangutans are responsible for concomitant differences in behavioural flexibility. The contribution by Holekamp *et al.* [133] suggests instead the existence of ultimately genetic constraints on the course of evolution based on their analysis of adaptations in limb and skull morphology in carnivores and primates. Thus, one needs to distinguish clearly between developmental and evolutionary constraints, which are both ultimately based on genetic information.

Despite the differences that define and separate closely related species, they also share many traits, including behavioural ones, as a result of common ancestry. This similarity can be quantified by the strength of the phylogenetic signal [134], which is also discernible at higher taxonomic levels, albeit with attenuated strength. These phylogenetic associations may be a consequence of past adaptations and may constrain the evolution of traits in contemporary species. However, they may also be a consequence of similarities in ecology, life-history parameters and social behaviour between related species, and their presence need not necessarily reflect the presence of evolutionary constraints. Comparative analyses can reveal patterns of phylogenetic signals above the species level, and Thierry [135], for example, describes sets of correlated traits that covary among phylogenetic subunits within the genus *Macaca*. By looking at a wide range of primates, Kamilar & Cooper [136] quantify the degree of phylogenetic signal in several behavioural and ecological traits, and discuss the possible mechanisms for this evolutionary diversity and why different behavioural traits have different relationships to phylogeny. As in other similar studies, however, we are still far from understanding the causes of phylogenetic signals.

### (b) Developmental constraints

Another set of constraints is based on the fact that genetic information and cellular components and processes shaping behaviour within-species is translated via developmental programmes into proteins, which in turn are combined to furnish the proximate agents underlying behavioural modulation such as hormones, neurons and muscles. Species-level consistency of these processes, which may ultimately underlie phylogenetic signals, can be brought about by a number of mechanisms, including insensitivity to environmental change, set-points in homeostasis, polygene genes, developmental canalization and the costs of maintaining continuous individual behavioural flexibility [15], which can be surprisingly low [130]. However, there is also variation in the behavioural outcomes of development among otherwise rather similar individuals, such as littermates, that are brought about by differential accommodation to the disruptions of normal development. The strength of such developmental variability has been revealed by a remarkable study of clonal crayfish raised under identical environmental conditions [137], but it remains poorly studied among mammals. Epigenetic modifications of genetic information can also result in modulation of offspring social behaviour in response to social or ecological stimuli during

early development [138,139], highlighting the fact that genetic and developmental mechanisms are inseparable and may often be closely linked to social and ecological ones.

This point is forcefully illustrated by Sachser *et al.* [140], who summarize the neuroendocrine processes affecting behavioural outcomes in rodents that operate throughout ontogeny, including the prenatal phase. The contribution by Faulkes & Bennett [141] further illustrates how group-level variation and species differences in social behaviour (among mole rats) are constrained by particular patterns of neurotransmitter expression and physiological control of reproduction. As emphasized by Schradin [130], physiological mechanisms of social flexibility can differ in their temporal impact: neuronal mechanisms can lead to very quick and short-lasting responses, endocrine changes take longer but might also last longer, whereas neuroendocrine changes are predicted to be the slowest and longest-lasting mechanisms. In general, however, it is still difficult to cleanly separate cause and consequence in such associations between developmental and behavioural contrasts.

### (c) Ecological constraints

The decades following Tinbergen's seminal paper have been characterized by an increasing theoretical and empirical focus on ecological factors as the main determinants of social behaviour. Research in behavioural ecology has identified predation risk as an important determinant of species differences in social organization, and the distribution and quality of food resources as a main determinant of interspecific variation in social structure. The failure of this verbal model to correctly explain or predict many patterns of mammalian social systems has been partly attributed to its primate bias [114]. However, Faulkes & Bennett [141] show that interspecific variation in mole rat social organization can be neatly linked to one environmental variable, in this case aridity. Ecological factors also explain variation in marmot social organization [142]. The above-mentioned socioecological model provides the starting point of a comparative analysis by Koenig *et al.* [143] in which they test predictions about links between ecology and mating systems among primates, scrutinizing the predictive power of socioecological models and demonstrating the necessity of testing and refining existing theoretical frameworks in social evolution. Ecological factors can also exert strong influences on intraspecific variation in social systems. As shown by Schradin [130] (see [144]), flexibility evolves especially in unpredictable environments with repeated similar changes, or in marginal habitats [145], selecting for genotypes that enable a broad reaction norm for social behaviour. A broad consensus appears to be emerging among behavioural ecologists, however, that ecological constraints on behavioural flexibility should no longer be studied in isolation of other factors [135,143].

### (d) Social constraints

It is perhaps not surprising that patterns of social behaviour should be importantly modulated by social factors. In recent decades, variation in social factors, such as variation in the distribution of females, has been studied primarily in the context of mating system evolution. Sexual conflict theory [146] provides a more recent example of considering interdependencies in social behaviour, in this case between males and females [147,148]. Moreover, kin selection theory has been

successful in explaining interindividual differences in social behaviour as a function of the presence of close kin [35,149]. There may even be interesting links between these two behavioural domains [150]. Several contributions to this Theme Issue highlight the fact, however, that many other aspects of social structure are also influenced and modulated by a variety of social factors.

For example, Sachser *et al.* [140] summarize evidence from experimental studies on rodents demonstrating that the social environment that an individual experiences during its entire lifetime, including the prenatal phase, has lasting effects on adult social behaviour, which, in turn, raises a suite of interesting questions about the underlying developmental and proximate mechanisms. Runcie *et al.* [151] examine the extent to which the expression of different genotypes is influenced by the social environment. Their studies on wild baboons reveal that social connectedness, maternal dominance rank, and group size all interact with genotype to influence gene expression not only in early life but also in adulthood. Using a long-term dataset, Blumstein [142] demonstrates that demographic dynamics impact several aspects of social organization and social structure in marmots. Henzi *et al.* [152] use detailed comparisons of female social behaviour between two populations of vervet monkeys with different group sizes to test the possibility that selection has acted on social reaction norms that encompass demographic variation both between and within populations. Cantor & Whitehead [153] analyse patterns of group-specific social behaviour transmitted by social learning among whales and dolphins to test the proposition that culture and social structure mutually affect each other. Montiglio *et al.* [154] summarize recent studies, many on non-mammals, showing that even consistent individual differences in behaviour can be affected by social interactions with conspecifics. The resulting notion of individual social niche specializations may provide

a fruitful avenue for future research into social determinants of individual variation in mammalian social behaviour. Here, as in other contexts, however, experimentation will eventually be required to separate causation from correlation when studying association patterns between social phenomena.

## 5. Conclusions

The explicit focus on all levels of explanation reveals how mammalian sociality is constrained by ecological, evolutionary, genetic and developmental factors. Admittedly, no single study has examined all these constraints simultaneously, but evaluating these studies together emphasizes the close functional and mechanistic integration of these constraints and the kinds of insights that might be gained from a truly Tinbergian approach. In addition, this reveals how constraints are crucial to the evolution and expression of behavioural flexibility and that, at present, we know more about individual behavioural flexibility than about flexibility in many social system components. The contributions to this issue demonstrate how a Tinbergian integration of different approaches to investigating animal social systems is beginning to materialize, how such integration can reveal new interrelationships between proximate and ultimate determinants of social behaviour, and why it should, therefore, be an important component of future research on the social systems of mammals and other taxa alike. We hope that this issue will contribute to this process.

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