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Social nutrition: an emerging field in insect science

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Special issue: "Social life in insects: can we get new insights from the "other" social insects?"

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Short title: Insect social nutrition

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Abstract

Nutrition is thought to be a major driver of social evolution, yet empirical support for this hypothesis is scarce. Here we illustrate how conceptual advances in nutritional ecology illuminate some of the mechanisms by which nutrition mediates social interactions in insects and some other arthropods. We focus on experiments and models of nutritional geometry and argue that they provide a powerful means for comparing nutritional phenomena across species exhibiting various social ecologies. This approach, initially developed to study the nutritional behaviour of individual insects, has been increasingly applied to study insect groups and societies, leading to the emerging field of social nutrition. We discuss future directions for exploring how these nutritional mechanisms may influence major social transitions in insects and other animals.

Keywords

Insects, nutritional geometry, social interactions, social evolution, comparative analysis.

Highlights

- Nutrition mediates a wide range of social interactions.
- Nutritional geometry is a powerful means to study these effects.
- This approach was first developed to study individual insects.
- It is increasingly applied to groups and societies.
- Comparative research will clarify the role of nutrition in social evolution.

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The geometry of insect nutrition

Over the past few years, growing attention in insect social behaviour has been dedicated to non-eusocial species that nevertheless exhibit sophisticated interactions and group structures (e.g. [1–3], see also the article by Costa in this special issue). Diversifying the scope of insect behavioural research is essential to assess the full diversity of social forms and open new lines of research with the aim of understanding how different evolutionary pathways may lead to social life [4].

Nutrition, which encompasses behavioural strategies related to food selection, acquisition and processing, is a striking example. Many authors have identified food constraints as potential drivers for insect social evolution [5–8]. For instance the transition from ancestrally solitary cockroaches to social wood roaches and even eusocial termites may have evolved in response to the challenge of acquiring sufficient nitrogen from diets dominated by wood [7]. However these nutritional effects have remained difficult to quantify and compare across eusocial taxa, which has long hampered the development of a unifying theory [9]. Here we argue that conceptual advances used to study nutrition in solitary and gregarious insects provide such a framework.

Insects, like humans, carefully select foods and consume them in quantities and proportion that maximise fitness [10,11]. Important insights about insect nutrition come from nutritional geometry (Figs 1A and 1B), a graphical modelling approach first developed by Stephen Simpson and David Raubenheimer to study dietary regulation behaviour by herbivorous locusts [12,13] (for recent reviews see [14,15]). In nutritional geometry, foods are defined by their key dietary components (typically, but not exclusively, proteins and carbohydrates). Individuals are defined by their nutritional state (NS) and their intake target (IT; e.g. optimal state). In this approach, it is therefore possible to predict the blends of foods an insect should eat in order to acquire mixtures of nutrients maximising fitness traits, and to test these predictions in experimental conditions where animals are given artificial diets [16,17].

Although initially applied to individual insects, nutritional geometry was recently extended to study the role of nutrition in social interactions (i.e. social nutrition) within groups and societies [18–20]. In this case, each individual has its own NS and attempts to reach an IT, either independently from the others (Fig. 1C) or by interacting socially or competitively (Fig. 1D). At the most basic level, animals may attract each other to feeding sites, potentially leading to collective foraging dynamics for nutrient balancing [21]. However more complex interactions may occur, as for instance in provisioning species, when adults must simultaneously choose foods to address their nutritional needs as well as the different needs of their offspring [22].

Here, we consider the emerging research field of social insect nutrition. We illustrate how nutritional geometry has been used to investigate some of the mechanisms that

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drive social interactions in a broad range of non-eusocial insects and some other invertebrates, and how this research increasingly motivates studies in eusocial insects. We discuss how comparing social phenomena based on the nutritional properties of groups (variance in NSs and ITs) may help delineate major principles by which nutrition influences social behaviour and evolutionary transitions.

Collective behaviour

Complex group dynamics often emerge through the repetition of simple social interactions [23]. In groups characterised by a low variance in NSs and ITs (Fig. 2A), nutrition can modulate these interactions and lead to collective movements.

Mass migrations

Outbreak orthopterans, such as locusts and crickets, exhibit mass migrations. In these insects, the homogenisation of the NSs of individuals (due to crowding) favours phenotypic changes and social interactions that trigger the onset of collective motion.

Short scale migrations of marching Mormon crickets (*Anabrus simplex*) and nymphs of desert locusts (*Schistocerca gregaria*) have been associated with a nutritional imbalance (or deficit in specific nutrients) [24,25]. During outbreaks, these insects congregate on receding vegetation patches [26], which in locusts induces a phenotypic shift from a solitarious to a gregarious phase. In these conditions of nutritional restriction, crickets [25] and locusts [27] seek out proteins (and mineral salts in the case of crickets) at concentrations matching those found in the tissues of conspecifics. By eating each other, insects can supplement their intake of nutrients that are limiting in the environment and increase their survival [28]. Cannibalistic interactions result in a push-pull mechanism in which insects move to reduce their risk of being eaten, while chasing ahead for potential victims, leading to the formation of marching bands at critical population densities [29,30]. Larger scale migrations of flying adults, however, have been associated with a nutritional balance [31]. In the Mongolian locust (*Oedaleus asiaticus*), adults artificially fed balanced (low-protein) diets have increased muscle size and fuel stores, and thus fly for longer than individuals fed imbalanced (very low- or high-protein) diets [31]. In the Eurasian steppe, heavy livestock grazing and grassland degradation (loss of organic N) promotes locust outbreaks by shifting plant nutrient content toward optimal low-protein diets favourable to migratory morphs [32].

Collective foraging

Group foraging insects make collective decisions often enabling individuals to increase their probability to select good (if not the best) available options [33]. When resources are not nutritionally balanced, efficient foraging implies that groups alternate between exploiting multiple nutritionally complementary foods [14]. In such

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conditions, the homogenisation of the NSs of individuals (due to social cohesion and collective feeding) generates collective patterns for nutrient regulation.

Fruit flies (*Drosophila melanogaster*) self-select foods in order to balance their intake of protein and carbohydrates [16,34]. Under high population densities, these insects respond to an aggregation pheromone mediating collective foraging decisions [35]. If given the task to find a balanced diet among several imbalanced diet options, groups of flies outperform single flies, indicating that social interactions enhance individual choices [36]. In such conditions, collective feeding synchronises the NS of all individuals, which generates collective switching between complementary diets [18,19]. In the nomadically foraging forest tent caterpillar (*Malacosoma disstria*), where social foraging involves trail following and social cohesion is therefore stronger, group foraging can lead to suboptimal nutritional decisions by which the individuals settle on the first food patch discovered [37]. Presumably, the limited tree-wide searching and short-distance recruitment of *M. disstria* reflects more of a group cohesion function that constrains location of high-quality patches and the nutrition of individuals in laboratory conditions, in contrast to the collective flexibility in social foraging exhibited by its central-place foraging congener *M. americanum*. Nutritional geometry models predict that different levels of social attraction can enhance individual decisions in environments with different food abundances and spatial distributions [38], suggesting that the suboptimal behaviours that can be observed in experimental conditions may be more adapted to natural conditions.

Nutritional immunology

Parasites, pathogens and commensals can all modify the IT of an insect, ultimately influencing its feeding decisions [39]. These effects can generate a high variance in ITs among group members and affect collective dynamics (Fig. 2B).

Self-medication

Insects exposed to parasites often change their feeding preferences, seeking out substances to overcome the infection. While best-described cases of self-medication involve the consumption of toxic minerals or secondary compounds [40], nutrient intake can also influence the immune response of insects and help them combat parasites [41–43]. The clearest evidence come from the African armyworm (*Spodoptera exempta*), an outbreak moth whose larvae feed on graminaceous plants [44]. Caterpillars fed high-protein diets are more likely to survive a baculovirus infection than caterpillars fed low-protein diets [43]. Accordingly, virus-challenged caterpillars given a choice between complementary diets eat more protein than controls [43]. A similar switch of dietary preferences has been modelled to explore the possibility of collective medication in eusocial insect colonies, whereby foragers adjust their nutrient collection to the ITs of infected (higher in protein) and non-infected nestmates [45]. In such social groups, large variance in ITs (due to different

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infection statuses among individuals) may generate complex dietary regulatory patterns. Although there is not direct demonstration of dietary collective medication in eusocial insects, honey bees (*Apis mellifera*) infected with the microsporidium *Nosema ceranae* tend to collect and eat pollens that are richer in protein, which increases their survival [46,47].

Gut microbiota

Many insects are nutritionally and immunologically dependent on symbiotic microbes [48]. An individual's diet influences its microbiota [49], which can in turn affect host physiology and behaviour, including food decisions [50] and social interactions [51]. In a host group, different microbiota communities can generate large variance in the ITs of individuals, potentially leading to collective patterns of nutrient regulation. In the fruit fly (*D. melanogaster*), microbes found in the food modify individual nutritional decisions [50]. When offered a choice between different diets, microbe-free flies choose a nutritionally balanced diet, whereas flies artificially supplemented with microbes tend to choose slightly imbalanced diets (high-protein or high-carbohydrate), depending on which microbes the flies were associated with [50]. Seeding diets with microbes further influences these foraging patterns, leading flies to trade-off between balancing nutrient acquisition and acquiring beneficial symbionts [50]. Interestingly, flies artificially supplemented with commensal bacteria do not express any negative symptoms following deprivation of essential dietary amino acids, indicating that microbes can also compensate for a nutritional imbalance [52].

Inter-individual behavioural variability

Advanced societies are characterised by some level of behavioural variability, sometimes leading to division of labour. In a group, differential access to nutrients among individuals can generate a high variance in NSs, underpinning behavioural variability (Fig. 2C).

Temporary roles

Socially foraging insects often alternate between feeding and moving phases in a coordinated manner [23]. In such groups, variance in the NSs of individuals can regulate the behavioural transition, whereby individuals with the greatest nutrient imbalance initiate feeding and lead groups. In the nomadic forest tent caterpillar (*M. disstria*), which forms foraging trails of dozens of individuals, most protein-deficient individuals tend to initiate collective departure and lead the group towards new feeding sites, whereas protein-satiated individuals follow behind [53]. Theoretically, this nutritional regulation of temporary roles can lead to collective patterns where the decisions to switch from one food to another nutritionally complementary food may emerge through natural variation in the NS among leaders (most imbalanced state individuals) and followers (most balanced states individuals) [19].

Reproductive division of labour

In addition to mediating temporary roles, differential nutrition generates variance in the NSs of individuals that can be associated with reproductive division of labour where only a subset of the individuals can reach their IT and become either dominant [54] or breeder [55]. Social spiders of the genus *Stegodyphus* form colonies in which less than half of the females reproduce. These spiders share large webs that allow them to capture bigger prey, but the largest females tend to monopolize limited nutritional resources required for growth and reproduction [56]. When artificially supplemented with lipid-rich prey, colonies produce higher proportions of reproductive breeders relative to non reproductive helpers, indicating that lipids determine the magnitude of reproductive skews in this species [57]. In more advanced societies, differential feeding, whereby adults selectively allocate nutrients to the larvae, has also been implicated in regulating the development of reproductive castes (e.g. eusocial hymenoptera [58], termites [7]). In the honeybee (*A. mellifera*), larvae fed royal jelly, honey and pollen develop into sterile workers, while larvae exclusively fed royal jelly develop into queens [59]. Similar effects have been observed in solitary bees (*Megachile rotundata*) suggesting that nutritionally regulated reproductive plasticity is an ancestral condition that facilitated social evolution in bees [60].

Foraging for others

Food provisioning implies that some individuals need to collect foods that address the divergent needs of multiple other individuals. In such groups, characterised by a high variance in NSs and a high variance in ITs (Fig. 2D), nutritional interactions can lead to complex foraging patterns.

Oviposition site decisions

When the nutrition of juveniles depends on parents, adults must make foraging decisions that simultaneously address their own IT as well as the different ITs of their progeny. At the most basic level, a female may choose to lay eggs in site providing good nutrition to the larvae. Female fruit flies (*D. melanogaster*) eat and lay eggs in decaying fruits. When selecting a food source, flies must therefore integrate decisions about feeding (individual nutrition) and egg laying (offspring nutrition). Flies given a choice between artificial diets varying in concentration and ratios of protein to carbohydrates exhibit complex food visitation dynamics, alternating between laying eggs on high-carbohydrate diets and feeding on different diets depending on their NS [36]. Although larvae show faster development when reared on high-protein diets, they survive better and reach higher learning performances on diets with more balanced protein to carbohydrate ratios [36]. The apparent mismatch between the oviposition preference of females for high-carbohydrate diets and the high performance of larvae on balanced diets reflects a natural situation were high-

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carbohydrate decaying fruits become enriched in high-protein yeast as they start rotting, yielding optimal nutrition for the developing larvae [61], suggesting that females select oviposition sites based on sensory cues predicting good larval nutrition.

Colony-level nutrition

In eusocial insects, foragers need to satisfy the ITs of all colony members, including themselves, the non-foraging workers, as well as the larvae and the queens, which have significantly higher protein needs [62]. Early applications of nutritional geometry in ants show that colonies dynamically regulate their protein to carbohydrate intake at a colony level IT [63] that can vary with colony composition [64]. If constrained to high-protein diets, ants reject excess protein in the form of pellets stockpiled in a waste dump outside the nest, which signals a need for carbohydrates to the foragers [64]. In these insects, variation in the ITs among castes modulate the complex network of social interactions within the colony including food assessment, collection, processing, storage and waste disposal [14]. Studies on bees show how colonies also balance their intake of free amino acids in nectar, and lipids and proteins in pollen, with important implications for understanding pollinator population declines [59]. For instance, honey bee colonies (*A. mellifera*) constrained to pollen deficient in one essential amino acid subsequently allocate more foragers towards the complementary diet in a choice test [65].

Farming

Some ants and termites farm ectosymbiontic fungi that turn nutrients into digestible food for the insects. Here, the divergence in the ITs of insects and the ITs of their cultivars structures the collective foraging pattern of colonies. In *Mycocepurus smithii* ants, for instance, fungal cultivars have conserved their capacity for independent reproduction [66]. Mapping fungus performance in a nutrient space revealed that the growth of edible somatic tissues and non-edible reproductive tissues are maximised on high-carbohydrate diets, but that modest protein provisioning can suppress reproductive tissues [66]. When given a choice between artificial diets, ants collect protein and carbohydrates in amounts and ratios that promote (but do not maximise) growth of fungal somatic tissues while inhibiting production of reproductive tissues to values that are consistent with field measures [67]. This nutritional control by ants reflects their need to curtail potential host-symbiont conflict over the independent reproduction of fungi.

Future directions

In this short review we have illustrated how nutrition impacts on many forms of social interactions and how these effects can be studied experimentally and theoretically using nutritional geometry. This conceptual framework is increasingly used to compare social interactions in insects exhibiting various levels of social complexity

and provides a powerful basis for comparative research on the mechanisms by which nutrition affects social interactions and their evolution, in order to fill a major gap in insect science.

As proposed in Fig. 2, using the nutritional characteristics of social groups is an objective approach to quantify and compare the effects of nutrition on social behaviour. Comparative research on insect social behaviour has suffered from a priori criteria to classify social levels, sometimes misleading about the real complexity of the social interactions exhibited by species [68]. Natural selection is expected to act on the intake targets of individuals [69] and therefore to shape the variance in intake targets within groups and societies [19]. Understanding social behaviour in groups with comparable nutritional structures (in terms of diversity of nutritional states and needs), can reveal the specific effects of nutrition on social behaviour, especially as we progress from populations of solitary individuals to more integrated societies. Importantly, both the variance of nutritional states and the variance of intake targets within a group can be modelled (e.g. Fig. 1) and experimentally quantified and manipulated, thereby providing ample opportunities to generate and test predictions in a wide range of species [14]. Models of nutritional geometry have already been used to explore the evolution of nutritional behaviours [19,20]. For instance, social foraging, mediated by varying levels of social attraction and alignments, is expected to be most adaptive in environments where food resources are imbalanced, abundant but recalcitrant, nutritionally rich but ephemeral, or patchily distributed, whereas solitary foraging should be favoured when food is dispersed [38], a result in line with theories about the evolution of food recruitment in eusocial insects [70]. Future work should explicitly include selection processes to generate scenarios by which nutrition may favour evolutionary transitions between different social forms.

The field of social nutrition is still in its infancy and many mechanisms by which nutrition shapes social interactions still remain to be discovered. Simple societies can teach us a lot about social behaviour and motivate important research in more advanced societies, as illustrated by fast growing research on social bee nutrition [59,71]. Since basic features of nutritional biology are shared by virtually all animal species, including humans [72], this approach has implications beyond just the insect sciences [73], and may provide key insights to study the broader role of nutrition in the evolution of animal societies .

Conflict of interest

None declared.

Acknowledgements

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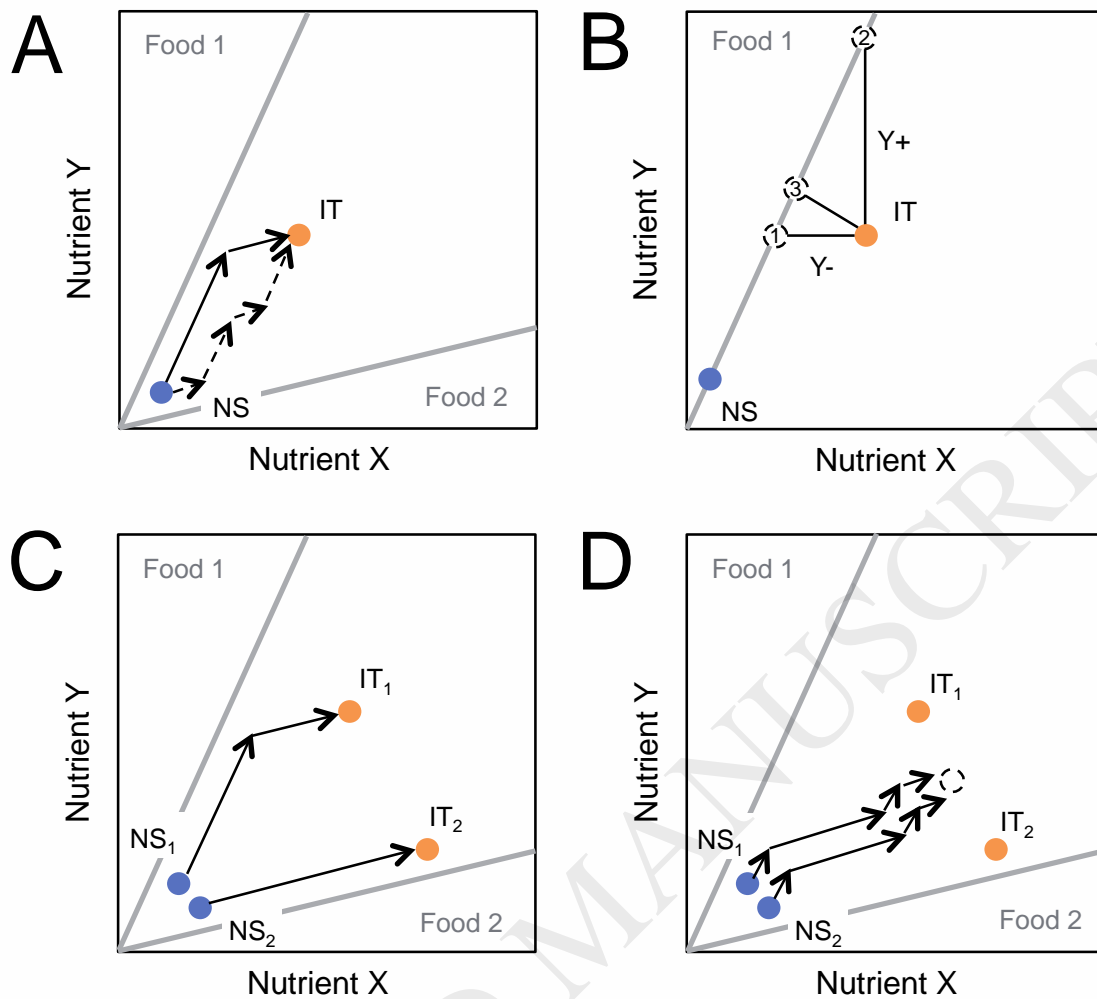
Fig 1. Examples of nutritional geometry models for hypothetical individuals (A and B) and groups (C and D). **A.** Nutritional rails (grey lines) represent the ratio of nutrients X and Y in foods. The blue dot is the nutritional state (NS) of the individual and the red dot is its intake target (IT). Foods 1 and 2 are individually imbalanced but complementary (fall on opposite sides of the IT). The individual can reach its IT by combining its intake from the two foods (arrows). **B.** The individual is restricted to a single imbalanced food and can: (1) satisfy its needs for Y but suffer a shortfall of X; (2) satisfy its needs for X but over-ingest Y; (3) suffer a moderate shortage of X and excess of Y. **C.** The two individuals have different NSs (NS_1 and NS_2) and ITs (IT_1, IT_2). In this example the individuals do not interact. Each individual can reach its IT by combining its intake from the two foods using a different foraging sequence. **D.** In this example the two individuals are socially attracted and move together from food 1 to food 2. In doing so, none of the individuals can reach their IT. However both can make a compromise to approach an area in the nutrient space minimising the distance between the two ITs (e.g. the collective IT, white circle). (A and B were modified from [14]).
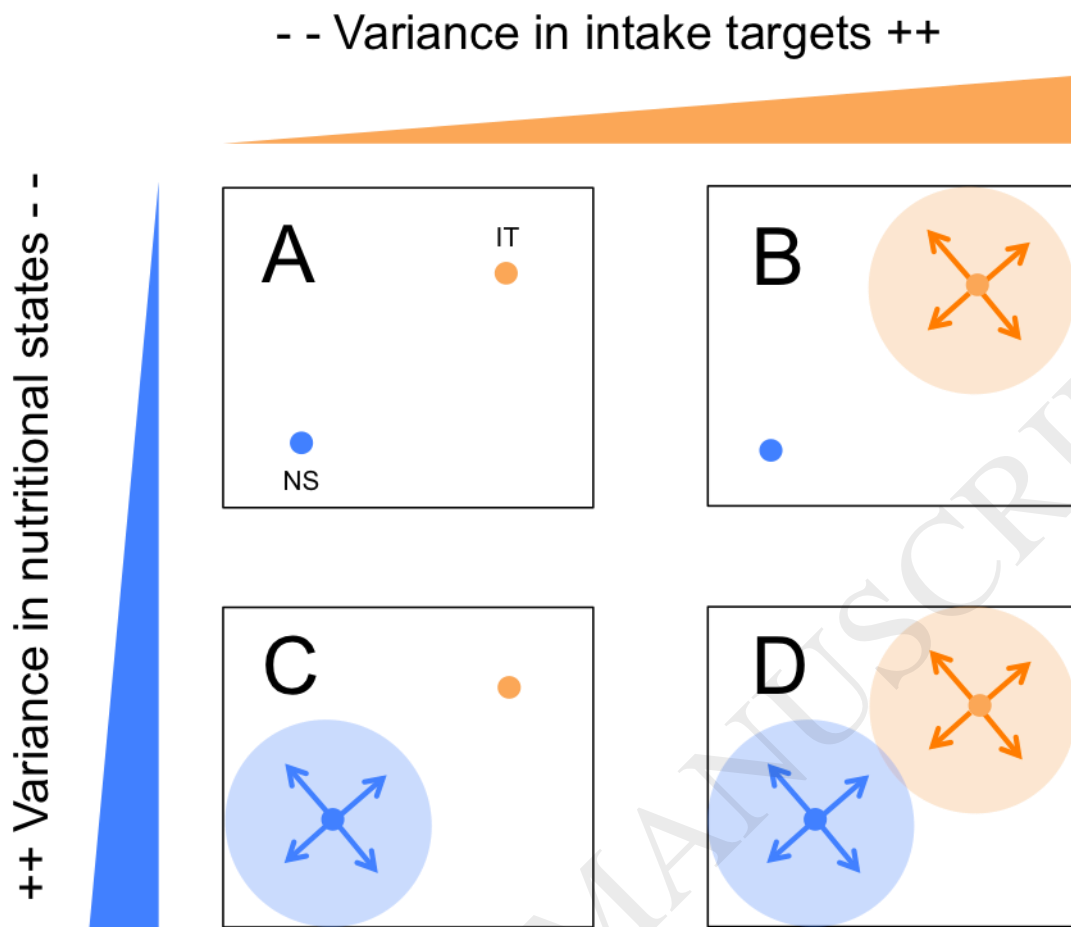
Fig 2. Comparing social interactions based on the nutritional properties of groups (variance in nutritional states, NS, and intake targets, IT). **A.** Individuals have the same NS and the same IT. This group structure favours collective behaviour (e.g. crickets and locusts, fruit flies, tent caterpillars). **B.** Individuals have the same NS and different ITs. This group structure is characteristic of host-parasite interactions (e.g. caterpillars, bees) and host-microbiota interactions (e.g. fruit flies). **C.** Individuals have different NSs and the same IT. This group structure is often associated with behavioural variability characterising temporary roles (e.g. tent caterpillars), and permanent division or labour (social spiders, eusocial bees). **D.** Individuals have different NSs and different ITs. This group structure is common in species displaying offspring habitat selection (e.g. fruit flies), food provisioning (e.g. eusocial ants and bees) or symbiont farming (e.g. fungus-farming ants).