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Review

Pre-emptive behaviour in a landscape of intergroup conflict

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Intergroup conflict is a powerful selective force throughout the animal kingdom. While research has traditionally focused on actions during and after contests, animals also exhibit behavioural flexibility in anticipation of potential intergroup encounters. Synthesising findings from diverse taxa, we describe how social species adjust pre-emptive information gathering, resource use, cohesion, synchrony, and intragroup interactions across a heterogeneous 'landscape of intergroup conflict'. We show how variation in threat level, driven by spatial context, rival characteristics, and individual motivation, affects these behaviours, and how balancing sensed information and memories of past interactions underlies associated decision-making. Testing the consequences of intergroup pre-emptive behaviour using experimental, technological, and analytical advances will develop understanding of its role in socio-cognitive evolution, population dynamics, and community structure.

Highlights

Humans are well-known for preparing for warfare in various ways, and it is increasingly apparent that other social animals also exhibit behavioural flexibility in anticipation of encounters with rival groups.

From ants to apes, there are examples of pre-emptive changes in surveillance, space use, raiding, affiliation, and cohesion that either inform decisions about whether to seek out versus avoid rivals or maximise the chances of winning any ensuing contests and thus gaining a benefit.

The threat presented by rivals depends on location, group characteristics, and individual motivations, which determine the extent of the anticipatory behaviours displayed.

Just as prey adjust their behaviour to a 'landscape of fear' generated by predators, animal groups modify their actions across a 'landscape of intergroup conflict', with social, spatial, cognitive, population, and community consequences.

A landscape of intergroup conflict

Intergroup conflict (see Glossary) is prevalent throughout the natural world, acting as a powerful evolutionary force across taxa [1–4]. In social species, groups often compete with **conspecific outsiders** who are seeking resources such as mates, breeding positions, food, shelter, and space [3,5,6]. **Intergroup contests** can have significant immediate and delayed consequences for individual fitness and group survival [7,8], and thus intergroup conflict exerts a strong selective pressure on animal behaviour. Traditionally, research has focused on actions during contests between rival groups—for example, interindividual variation in participation and factors determining who wins [5,6,9]—and the behavioural consequences in the aftermath, including changes in intragroup affiliation, movement patterns, and resource use [10–12]. However, there is an emerging awareness that evolution can also select for **pre-emptive behaviours** that optimise the likelihood of encountering rivals and maximise the chances of winning any ensuing contests—anticipatory behaviours that occur before, and even without, any current interaction with another group.

In general, pre-emptive behaviour includes relatively fixed actions in preparation for future events that occur in response to specific environmental cues. For example, various bird species migrate or store food to mitigate forthcoming winter conditions, with these behaviours initiated by a reduced photoperiod. However, our focus in this review is behavioural flexibility in response to more rapidly fluctuating circumstances; whilst the seasons change reliably, particular social interactions might not happen at all and can vary greatly in their occurrence across time and space. It is well established that prey species alter, for instance, their travel routes and vigilance–foraging trade-offs to minimise predation risk, drawing on spatial and temporal variation in information about the '**landscape of fear**' to aid decision-making [13,14]. Social species should similarly adjust their behaviour according to the '**landscape of intergroup conflict**' arising from the heterogeneity in threat posed by conspecific outsiders [15,16]; rivals can vary

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hugely in their competitive ability and motivations [3,17–19], generating a nuanced threat landscape.

Pre-emptive behaviours are important to consider because the threat of conflict is more pervasive than the often-infrequent contests themselves. Moreover, pre-emptive behaviours could affect individual fitness, group distributions, population density, and community-level processes in ways that do not obviously link to contests themselves. As with the landscape of fear, navigating a landscape of intergroup conflict has implications for future planning, spatial memory, and therefore cognitive evolution, but there are also unique consequences for territoriality, group dynamics, cooperation, and sociality. Whilst humans have long been known to exhibit pre-emptive behaviour in an intergroup conflict context—preparing for warfare by increasing surveillance, using elevated areas to gather information, showing greater affiliation and cohesion, conducting ambushes and raids, and moving quietly through enemy territory to avoid detection [20–23]—recent studies of wild animal groups provide analogous examples of many of these behaviours. Studying other species experimentally and in natural conditions can therefore help to provide insights into our own conflict ancestry.

Pre-emptive behavioural changes and potential benefits

In anticipation of encounters with rival groups, nonhuman animals adjust various behaviours to enhance information gathering, incentivise contest participation, reduce anxiety, and minimise collective and individual risk. **Interactive displays** between rivals can be described as 'pre-emptive' in a broader sense (e.g., pre-contest assessment of rival strength during vocal or visual exchanges), but our focus is behaviour before any direct engagement with outsiders. To illustrate our ideas, we provide examples from diverse social species across the animal kingdom; some of the identified pre-emption is present in animals that defend resources as individuals or pairs, but we concentrate on group-living species as they can exhibit a wider range of behaviours including interactions between groupmates.

Information aids decision-making [24], so selection should favour behaviours that allow more informed tactical choices about engagement with intergroup rivals (e.g., whether to advance or retreat) and preparation for potential contests (e.g., how much to invest in intragroup cohesion). For example, just as slower movement with intermittent pausing increases predator sensing [25], slower-moving groups might better detect rival vocalisations or scent cues. Likewise, minimising engagement in noisy activities may enhance acoustic information gathering and reduce a group's own detection by rivals, whilst adopting elevated positions could provide both longer lines-of-sight and improved long-distance sound detection. Detailed observations indicate that chimpanzee (*Pan troglodytes verus*) groups are more likely to climb hilltops when travelling towards areas where intergroup contests occur; on hilltops, groups engage in more resting (which is not due to the hill-climbing *per se*), rather than noisier feeding or travelling [15]. Experimental increases in intergroup threat caused dwarf mongooses (*Helogale parvula*) to move slower, interact for longer with scent marks, and conduct more sentinel (raised guarding) behaviour when they can monitor the area more easily (Figure 1). Information about rivals often informs immediate decisions [15,29], but may also update baseline prior knowledge about neighbour characteristics (Figure 2). Moreover, individuals can travel considerable distances to eavesdrop on the contests of other groups to gather social information that is used only days or weeks later, as seen in acorn woodpeckers (*Melanerpes formicivorus*) [30].

Intergroup threat can affect the relative use of different areas. Contest costs [7] mean that animals should avoid unnecessary encounters where possible. Groups of Japanese macaques (*Macaca fuscata*) and long-tailed tits (*Aegithalos caudatus*), for example, use areas shared with rivals less

Glossary

Collective-action problem: a collective effort (e.g., an intergroup contest) where nonparticipation by some group members reduces the likelihood of the group's success.
Conspecific outsiders: other individuals, subgroups, or full groups of the same species who threaten the resources of a particular group of individuals.
Free-riding: when an individual benefits from a shared outcome (e.g., winning an intergroup contest) but does not contribute their fair share of the costs (e.g., time and risk from participation).
Interactive displays: back-and-forth signalling (e.g., visually or vocally) by rivals.
Intergroup conflict: disagreements (i.e., conflicts of interest) between members of different conspecific groups over resources such as territorial space, food, mating opportunities, or breeding positions.
Intergroup contest: an aggressive interaction event between a group and one or more conspecific outsiders, where each party attempts either to defend or gain access to indivisible resources.
Landscape of fear: spatiotemporal variation in the perceived threat posed by predators. Generally, increased predator presence equates to increased risk and, thus, for instance, increased vigilance and avoidance.
Landscape of intergroup conflict: spatiotemporal variation in the threat presented by conspecific groups. Groups might choose to approach or avoid areas and either increase or decrease other behaviours, depending on the relative threat presented by a particular rival.
Pre-emptive behaviour: actions taken in advance of a specific event; in the case of intergroup conflict, before a potential contest with conspecific outsiders. The initial stages of an intergroup interaction may include pre-emptive assessment of relative strength (including from interactive displays), but the focus in this review is on actions taken prior to any such event and often in the absence of a rival.
Raiding: actively seeking out rivals when intruding into the area occupied by them; we do not include, in our definition, intrusions made to seek resources such as food.

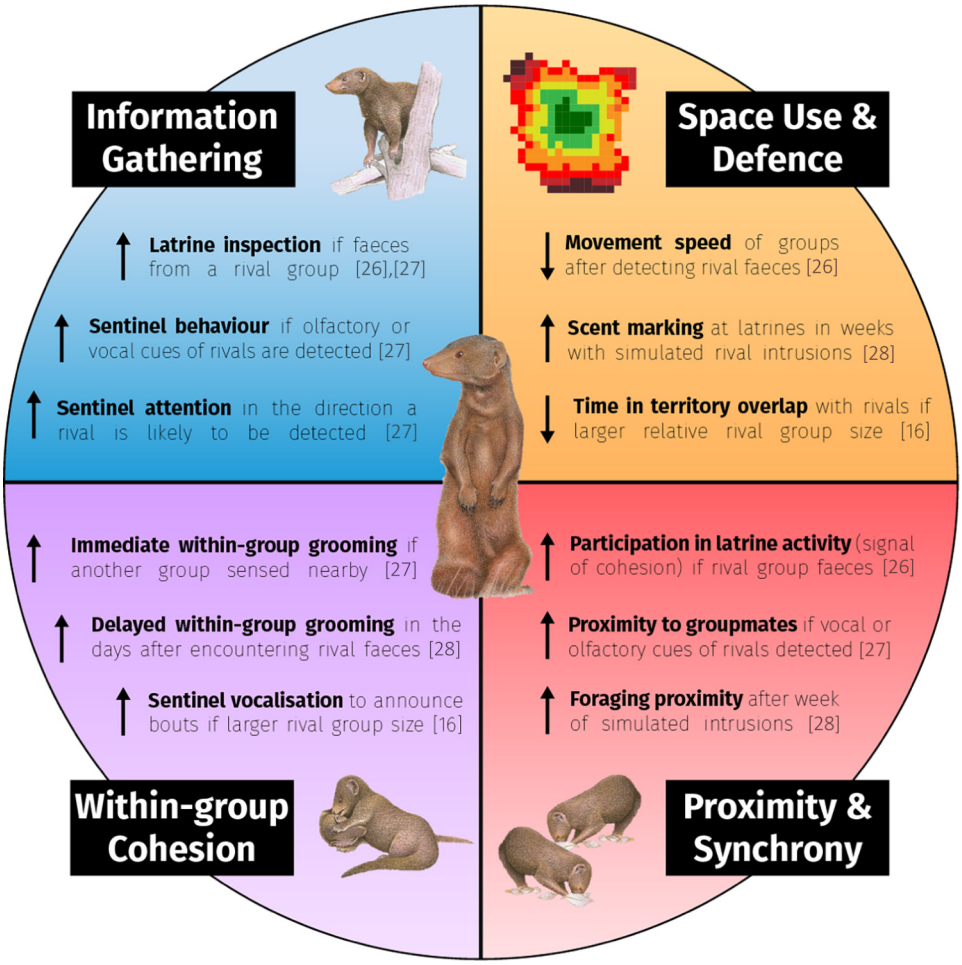


Figure 1. Pre-emptive behaviour of dwarf mongooses in an intergroup context. Immediate [26,27] and cumulative [28] responses to experimentally elevated intergroup threat (call playbacks and faecal presentations of rival groups). Behavioural changes in areas where intergroup contests are more likely and on borders where neighbours have a relatively larger group size [16]. Mongoose drawings by Martin Aveling.

Social buffering: the reduction in anxiety experienced by an individual due to the presence or behaviour of others.
Social incentives: an act (e.g., allogrooming) that encourages another individual to behave in a certain way to the benefit of the actor (e.g., participating in a subsequent intergroup contest).

than expected by chance [31,32], whilst chacma baboons (*Papio ursinus*) detour to avoid encountering groups detected nearby [33]. By contrast, increased use of shared or valuable areas can be beneficial in intergroup contests through a home-field advantage [10], or it can result from groups attempting to detect intruders and/or announce ownership using vocalisations or scent marks when patrolling territorial boundaries [34–37]. Such signalling should increase when the intergroup threat level is elevated, and dwarf mongooses engage in more latrining (depositing of scent marks) in response to experimental simulations of rival intrusions (Figure 1). Olfactory signals might also be positioned strategically: for instance, meerkats (*Suricata suricatta*) scent-mark disproportionately near burrows, as this is a resource examined by intruders [36]. Similarly, with acoustic signalling, black howler monkey (*Alouatta pigra*) groups return to past contest locations in a goal-directed manner, potentially to advertise their presence at locations recognisable to neighbours [34]. Beyond space-use patterns within a commonly used area (e.g., a home territory), a more extreme pre-emptive behaviour is **raiding** into space occupied by rivals and actively seeking them out (Box 1).

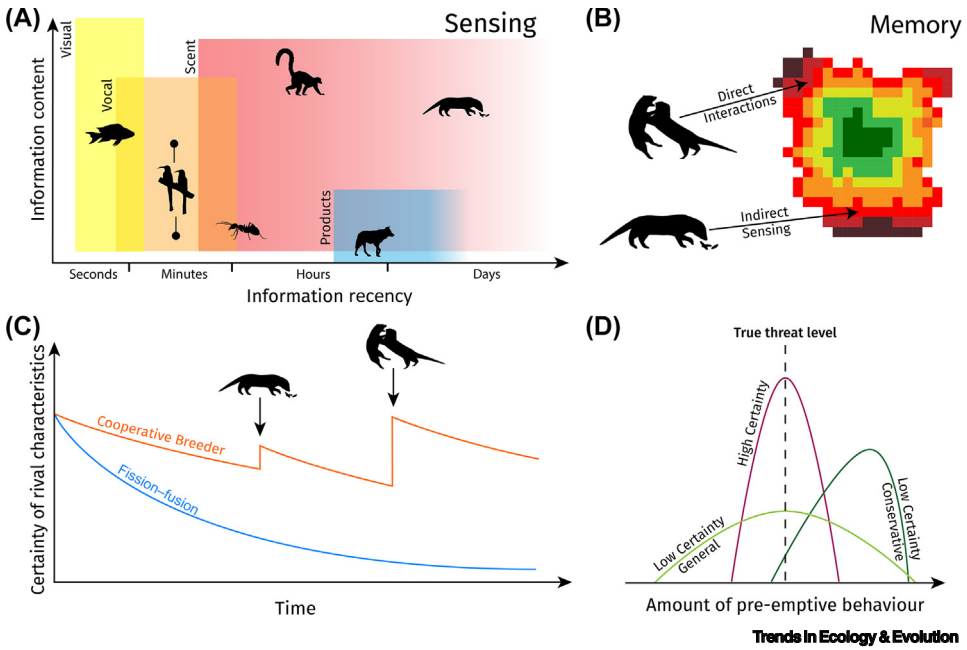


Figure 2. The information pathways animals use to guide pre-emptive behaviour. (A) Content and recency of different primary and secondary sensing. 'Information content': any aspect of rival characteristics (e.g., group size and sex ratio). 'Information recency': timeframe over which detection informs about rival presence. 'Scent' and 'products' (e.g., fruit husks) fade as the cue itself decays. Silhouettes illustrate examples, from left to right: cichlids see neighbouring groups; woodhoopoes hear neighbour alarm calls (low content) or territorial choruses (high content), illustrated by silhouette arms; ants detect rival pheromone trails; lemurs determine neighbour reproductive state from scent deposits; wolves find carcasses killed by neighbours; dwarf mongooses gain neighbour sex and body-size information from latrines. Many species can occupy multiple areas of parameter space. (B) Memories of previous direct and indirect information form the basis of a landscape of intergroup conflict; colour represents intergroup threat level in that area. (C) Current sensing and memories of past interactions integrate to form the certainty a group has about the characteristics (e.g., group size) of its rivals. Reliability of information, and therefore certainty, decreases over time with decay dependent on the social system. Memories alone may guide behaviour in the absence of sensed information; direct interactions or indirect sensing will update information to increase certainty about characteristics, but by different amounts. (D) The certainty of the threat posed by rivals will affect pre-emptive behaviour. For a given threat, high certainty should produce well-matched behaviour, whereas low certainty may result in more variable behaviour (general) or higher levels of pre-emptive behaviour to buffer against a potential larger threat (conservative).

In the face of elevated intergroup conflict, increased spatial cohesion and behavioural synchrony can provide various benefits. When the threat from outsiders is greater, groupmates of various mammal species stay closer to one another [44,45] (Figure 1), whilst green woodhoopoe (*Phoeniculus purpureus*) group members are more likely to roost together [46]. There can also be active recruitment: for instance, banded mongooses (*Mungos mungo*) and meerkats vocalise to recruit others when encountering latrines containing recent evidence of rival-group activity [47,48], and chimpanzees detecting another group drum on buttress roots to attract the attention of groupmates [49]. Recruitment can be context-dependent: for example, threatened turtle ant (*Cephalotes rohweri*) groups reduce the movement of soldiers to nests with large entrances (which are harder to defend), focusing on those that are easier to retain [50]. Spatial cohesion likely facilitates intragroup communication and information exchange; closer proximity to others can also reduce anxiety via **social buffering** [51]. Behavioural synchrony may have a similar bonding function via the release of analgesic and reward-inducing endorphins [52]. Synchronous activities can additionally signal cohesion, as with bottlenose dolphin (*Tursiops aduncus*) male alliances [53]. An extreme case in some army ant species (e.g., *Eciton burchellii*

Box 1. Raiding

Whilst all intrusions into areas occupied by other conspecifics to obtain resources could be described as 'pre-emptive' to some extent, a special case concerns 'raids', where the goal appears to be the seeking out of rivals themselves and not just, for instance, food.

The most extreme example is targeted killing: by reducing the current fighting force of a rival, groups can increase the chances of expanding their own resource base, recruiting new females, and reproducing successfully. Famously, male coalitions of chimpanzees (*Pan troglodytes verus*) undertake coordinated incursions (silently, in single file) into neighbouring territories with the apparent intention of attacking rivals, evidenced by them moving towards sounds of the other group's vocalisations [38]. Similar lethal gang attacks occur in various other mammals (see [39]).

Raids to kill offspring in rival groups occur in species such as banded mongooses (*Mungos mungo*) and greater anis (*Crotophaga major*) [17,40]. In anis, groups evict eggs from a rival's nest; in almost all cases, this results in abandonment by the targeted group and thus reduced food competition for the attacking group [17]. By contrast, honey ant (*Myrmecocystus mimicus*) and fire ant (*Solenopsis invicta*) workers in young colonies raid nearby conspecific nests to steal brood and thus augment their future workforce [41].

Raids can also be attempts to create opportunities: for instance, dampwood termites (*Zootermopsis nevadensis*) tunnel through to another colony, potentially aiming to merge and thus gain the advantages of a larger group size [42]; if the dominants are killed in a contest, creating a breeding vacancy, this can result in a further benefit to some individuals. More generally, in many species, the active seeking out and winning of contests may reinforce a pattern of intergroup dominance that has later benefits through winner-and-loser effects [43].

and *Labidus praedator*) involves multiple individuals standing side-by-side and posturing in the threat direction, thus forming a living boundary that reduces aggressive intergroup interactions [54]. Closer proximity to groupmates also means a larger potential fighting force if a physical contest develops; victory can require coordinated timing and intensity of actions [55,56], and widely scattered individuals are more easily outnumbered or outmanoeuvred with potentially lethal consequences [5].

Beyond spatial cohesion and behavioural synchrony, individuals may actively attempt to increase groupmate participation in a future contest. This is important because relative group size often drives contest outcomes, and maximising a fighting force requires solving **collective-action problems** [57]. Most obviously, there can be the use of **social incentives** (potentially underpinned by hormonal changes): for instance, chimpanzees groom and play with one another more in advance of collective territory defence [58,59], whilst green woodhoopoes increase allopreening when the intergroup threat is greater [46,60]. Experimental presentation of vocal and olfactory cues from rival groups led to greater allogrooming between dwarf mongoose groupmates (Figure 1). Aggression can also be used to increase subsequent contest participation by reticent individuals, as seen in vervet monkeys (*Chlorocebus pygerythrus*) [61]. Alternatively, within-group behaviours might be used to inhibit participation in intergroup contests. For example, male vervet monkeys who have sired current offspring (which might be vulnerable during fighting) or who want to assess dispersal opportunities through peaceful mingling with another group use physical aggression to prevent their female groupmates from instigating intergroup contests [62].

Variation in intergroup threat level

A baseline level of pre-emptive behaviour (e.g., time invested in seeking information, patrolling, and intragroup affiliation) will have evolved in a given species. However, to minimise the risk of costly contests with rivals, plasticity is expected depending on the current intergroup threat level. Threat level can vary depending on the location of the likely encounter and group characteristics, whilst group members may perceive the threat level differently depending on interindividual variation in potential costs and benefits.

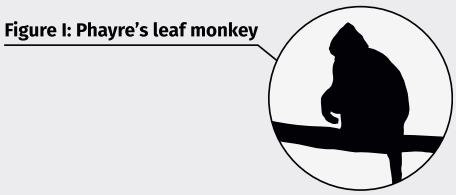
In general, pre-emptive behaviour should be greater where contests are most likely; for territorial species, this is often in peripheral versus core areas [12,16]. However, if secondary cues indicating the recent presence of rivals are discovered, then a threat might be deemed even higher in the territory core, nearer valuable resources or, in the case of neighbours, when they appear in an unexpected place [35,63]. Chimpanzees enter peripheral areas in larger parties than when moving elsewhere [64], Thomas's langurs (*Presbytis thomasi*) exhibit greater vigilance in overlap zones with neighbours [65] and green woodhoopoes allopreen more where contests with rival groups are more likely to occur [60]. However, care is needed with interpretations of location-based data, as simple null models of movement can often indicate lower use of peripheral areas [66]. There could also be edge effects: food abundance, predation risk, vegetation density, and anthropogenic pressures—not just intergroup threat—may differ between the edge and centre of territories, and thus explain observed behavioural differences [67,68].

Intergroup threat level also depends on various absolute and relative group characteristics (Box 2). Most obviously, relative group size affects contest outcomes: larger groups tend to beat smaller ones in many mammals and birds [5,73,74], though **free-riding** (when some group members do not participate and rely on the actions of others) can result in victories by those of intermediate or even smaller size [75,76]. Game theory predicts that animals should therefore evaluate the strength of potential opponents, as well as themselves, before approaching [9,77]. Indeed, chimpanzees, lions (*Panthera leo*), and spotted hyenas (*Crocuta crocuta*) use vocalisations to assess rival numbers from a distance, approaching only when there are favourable numerical odds [78–80]. More broadly, dwarf mongooses exhibit several pre-emptive behaviours that depend on the relative group size of the neighbours they risk encountering (Figure 1), whilst larger African wild dog (*Lycaon pictus*) packs prioritise scent-marking when in the territories of similarly sized competitors but not those of smaller packs [19]. Over a longer timeframe, smaller colonies of *Zootermopsis nevadensis* termites invest in 'faecal fortresses' as barriers to intrusion by larger colonies [81]. Factors such as relative group size do not operate in isolation (Box 2): for instance, whilst white-faced capuchin (*Cebus capucinus*) group size is most important on the periphery of a territory, home advantage plays a larger role in core areas where the costs of losing are greater for the resident group [63].

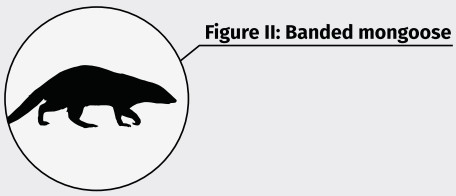
Threats and opportunities arising from intergroup contests vary amongst group members due to differences in relative costs and benefits [5], so pre-emptive behaviours are not expected to be conducted equally by all individuals. In white-browed sparrow weavers (*Plocepasser mahali*), dominant males face extra-group threats to both their position and paternity, so they disproportionately increase sentinel effort compared to their groupmates when the threat from outsiders is greater [82]. Certain individuals might also seek additional information (e.g., mating or dispersal opportunities), which could explain why subordinate male meerkats conduct the most sentinel duty when other groups are potentially nearby [83]. In terms of movement, banded mongoose females lead their group into rival territories to seek extra-group matings, with males paying the costs of ensuing contests as they are most heavily involved in the fighting [70]. To assess the composition of a rival group for dispersal options, young adult male crested macaques (*Macaca nigra*) sometimes leave the main body of their own group, which negatively affects spatial cohesion and behavioural synchrony (Waterman, J.O. PhD thesis, Liverpool John Moores University, 2021). Particular groupmates might be targeted with social incentives if their help is especially valuable. For instance, subordinate green woodhoopoes contribute more to contests and receive more allopreening from dominants in zones of intergroup conflict [60], whilst in primate species where males are larger than females and can make a bigger difference in intergroup contests, females recruit males as 'hired guns' by providing social support and copulations [84].

Box 2. Group characteristics that affect relative threat level

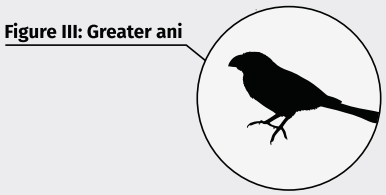
Group composition (e.g., sex ratio). In Phayre's leaf monkeys (*Trachypithecus phayrei*; Figure I), only males participate in intergroup contests: one-male groups most frequently used border areas without neighbours, whereas a multimale group was mostly present in areas with neighbours [69].



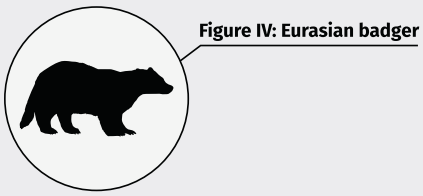
Reproductive stage. Banded mongoose (*Mungos mungo*; Figure II) females in oestrus are more likely than at other times to lead their group into rival territories to initiate intergroup contests and gain potential extra-group mating opportunities [70]. Groups are less likely to use overnight dens in areas where rivals may be encountered when they have vulnerable young [12].



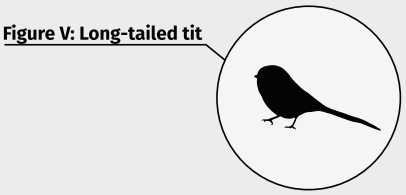
Tenure duration. Greater ani (*Crotophaga major*; Figure III) eviction of eggs from a rival nest is most often by groups who have been in the area for some time targeting new arrivals, and this effect increases with the number of years that the attacking group has nested there [17].



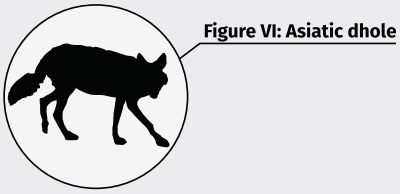
Neighbour versus stranger. When encountering experimentally presented faeces from rival groups, banded mongooses gave more worry calls to recruit others in response to cues from neighbours than strangers [47], whereas Eurasian badger (*Meles meles*; Figure IV) groups showed heightened behavioural responses towards stranger scents but not to those of neighbours [71].



Relatedness. In addition to an influence of relative group size, there is a negative relationship between avoidance of other flocks and the number of kin-connections between the groups in nonbreeding long-tailed tits (*Aegithalos caudatus*; Figure V) [32].



Factors acting in combination. For instance, as evidenced from a faecal-presentation experiment, the intensity of response to neighbours decreases and that to strangers increases with increasing pack size in Asiatic dholes (*Cuon alpinus*; Figure VI) [72].



The cognition of pre-emption

Animals have access to many sources of information through the sensing of primary and secondary signals and cues, as well as memories of past encounters. This information encompasses the likelihood of an interaction occurring (i.e., threat immediacy) and rival characteristics that influence threat severity. The quality, and therefore reliability, of information decays over time, both as past

information becomes outdated and as cues/signals and memories fade. To understand how all this potential information leads to a pre-emptive behavioural change, we need to consider how animals sense, process, retain, and act on information about outsider threats. This will then give us a better understanding of how intergroup conflict impacts cognitive evolution.

One form of information about the current intergroup environment comes from the sensing of primary cues, where animals can see or hear conspecifics before any direct interaction with them [15,85] (Figure 2A). Primary information provides the greatest certainty about threat immediacy, although in some cases (such as hearing distant vocalisations) there can be uncertainty about the exact location of rivals. However, information relating to threat severity can vary greatly: for instance, group chorusing can inform about rival-group identity, size, and composition, but there is likely little such information available when overhearing an individual conspecific alarm calling [35,86] (woodhoopoe silhouette—Figure 2A).

Many species also leave widespread secondary cues and signals in the environment (Figure 2A). Detecting a carcass or fruit husks may suggest little more than the recent presence of conspecifics. By contrast, scent marks can contain a wealth of information about the characteristics of those who deposited them, including the number of markers, their body size, sex, and reproductive state [9,87,88]. Secondary cues have the advantage of being detectable for much longer than primary cues. However, as they decay, this generates uncertainty both in how easily the information is assessed (e.g., as volatile compounds break down) and how reliable it is even if assessed correctly (e.g., characteristics and locations of groups change). Integrating knowledge from sensory ecology with our understanding of assessment strategies [9] will help generate testable predictions regarding what information animals are gathering and how reliable they perceive it to be.

Information about the likely location and characteristics of rivals can also be recalled from past interactions to guide current pre-emptive behaviour. The most obvious interactions will be those directly with rivals, but animals are also known to retain memories of interactions with scent cues [87], integrating these into an olfactory landscape [88]. Memories of past interactions can be conceived as a spatial map of intergroup threat, analogous to the landscape of fear [13,14] (Figure 2B). Such stored information can inform behavioural decisions in the absence of current primary or secondary cues or be remembered to supplement sensed information (Figure 2C). For instance, hearing a rival can reveal their presence, but recall of past interactions may be required in at least some species to assess their identity, size, and other characteristics (Box 2) that generate the perceived level of threat severity. Like secondary cues, the reliability of memories will decay over time, but the decay rate will be influenced by factors such as the social system (Figure 2C). In cooperatively breeding species, groups often move cohesively and have stable compositions [89,90], meaning information continuity over weeks or even months. By contrast, information from previous encounters will be less likely to accurately reflect a current threat in species that live in larger, more dynamic fission–fusion groups [15,80]. Similarly, living in more dynamic social systems makes it harder for individuals to assess their own current fighting force, increasing the challenge of determining the relative level of intergroup threat. Certainty about the current threat level is expected to influence the amount of pre-emptive behaviour shown; low certainty may result in more variable behaviour or could lead to higher levels as a bet-hedging strategy against the worst-case scenario (Figure 2D).

Statistical decision theory provides a valuable framework for considering pre-emptive decisions [24,91]. Past experiences act as informative priors, whilst sensed inputs integrate with these memories to form a posterior estimate of current threat through Bayesian updating, thus guiding

pre-emptive behaviour. Bayesian approaches have recently been used to increase our understanding of how animals make decisions regarding many aspects of behaviour [92], including in contests [93]. The weighting of each input depends on both its reliability and the cost to gather and process, whilst the decay of priors is governed by the reliability of the information type in the species in question. Previous experience and knowledge likely pertain much more to neighbours than strangers, which could generate differences in the balance in the use of cue information and memories depending on rival identity.

Testing of pre-emptive behaviour and its consequences

Furthering our evolutionary understanding of pre-emptive behaviour in the context of intergroup conflict, and the underpinning cognitive apparatus, requires experimental testing. Evidence already exists that various species change their immediate behaviour following the presentation of rival-group faeces [26,47]; the next stage would be the manipulation of the landscape of conflict. For instance, this could involve using repeated presentations in specific areas to alter the perceived threat level and to examine behavioural changes in the following days. However, doing so is logistically challenging, and there are ethical considerations, especially as intergroup conflict can cause stress and have lasting consequences [7,8]. Recent methodological advances allow for the unpicking of the neurological bases of social interactions across space [94]. Such approaches may help disentangle the responses to primary and secondary cues of rival presence from spatially anchored memories of outsider interactions, as well as identify which brain regions are important in pre-emptive decision-making. Technological improvements in GPS telemetry, biologging, accelerometers, camera traps, and passive acoustic recorders for the collection of animal movement and geospatial data could allow for the quantification of spatially explicit risk landscapes. Moreover, this could enable the analysis of the simultaneous space-use patterns of rival groups, as has been done with predators and prey [95].

Currently, there has been little testing of how pre-emptive behavioural changes influence either subsequent decision-making or contest engagement. For instance, we know of only one explicit example of how information gathered ahead of potential contests is used: chimpanzees assess from hilltops how far away rivals appear to be, using that information to inform tactical decisions about advancing or retreating [15]. Similarly, there is limited knowledge about how within-group behavioural changes affect subsequent contest contributions. In vervet monkeys, males receiving more affiliation or aggression from females are more likely to participate in the next contest bout [61], but experimental tests are lacking. It is feasible, in dwarf mongooses, for example, to manipulate either actual within-group aggression levels by providing large desirable prey items to subordinates—inducing aggressive chasing and stealing by a dominant [96]—or perceived levels of within-group aggression by playback of calls associated with foraging displacements [97,98]. Likewise, anti-parasite solutions can be applied to individual meerkats, reducing their ectoparasite load and thus manipulating allogrooming (affiliation) levels [99]. In each case, the goal would be to determine how those intragroup changes affect the occurrence of, participation in, and outcome of natural intergroup contests or the responses to the presentation of taxidermy models in association with relevant call playbacks as an experimental simulation of a rival intrusion.

Concluding remarks and future perspectives

Intergroup conflict exerts a pervasive selection pressure not only through direct contests but also via the need to produce pre-emptive behaviours in the absence of current interactions with rivals. Whilst there is emerging evidence of intergroup cooperation in a few species [100], which could influence the anticipatory behaviours observed before encountering a conspecific group, our focus has been on the intergroup conflict that is widespread across social species. Spatiotemporal variation in the likelihood and severity of intergroup encounters

Outstanding questions

In some species, such as stingless bees and ants, threats can come from both conspecific and heterospecific groups. Does the former drive more dynamic pre-emptive behavioural strategies rather than constitutive changes, such as the production of soldiers and toxins?

Some species exhibit intergroup cooperation as well as conflict. How does that dual relationship influence pre-emptive behaviours?

Do smaller animal groups make pre-emptive strikes against larger rivals, rather than avoiding them, to benefit from the element of surprise and thus help overcome unfavourable numerical odds?

If attacks are a surprise, defenders may not have the opportunity to prepare in the short-term. Equally, if defence is intrinsically more motivating, there might be a greater need for pre-emptive inducement in groups preparing to attack. Does pre-emptive behaviour, therefore, differ between attacking and defending groups?

How do group members coordinate their behaviour into effective joint actions before any intergroup contests, and what is the neurohormonal basis of coordinated actions?

Especially in species where lethal intergroup contests are relatively common (e.g., chimpanzees and banded mongooses) and mortality risks are high, are pre-emptive actions stronger both compared to other species and in relation to the actual threat of a contest?

Could commonly observed behaviours, such as playfighting and alliance formation, serve as longer-term preparations in an intergroup context?

What are the cognitive demands associated with pre-emptive actions? In which social systems and circumstances does intergroup conflict place the largest selection pressure on cognition associated with pre-emption?

Box 3. Implications of pre-emptive behaviour across different biological scales

Behavioural changes are unlikely to be cost-free, and there will be trade-offs against optimum actions in other contexts. For example, investing more in patrolling and scent-marking can come at the expense of feeding [19]. By contrast, the increased vigilance associated with intergroup conflict could synergistically aid in the detection of predators [102].

In turn, conflict-induced increases in vigilance have the potential to generate knock-on fitness consequences, such as better pup survival and thus adult reproductive success [102]. More generally, elevated intergroup threat, especially over an extended period, can cause chronic stress; behavioural changes arising as a consequence can result in reduced reproductive success [103].

Impacts on individual fitness will feed into population dynamics. Predator-driven landscape-of-fear effects on populations are predicted to be most pronounced in highly heterogeneous landscapes [13]. Intergroup conflict generates such heterogeneity because the threat posed by rival groups varies both spatially (e.g., across a territorial gradient from core to edge) and temporally (e.g., due to differences in the same neighbouring group at different times).

These effects of a landscape of intergroup conflict could also be felt at the community level through behaviourally mediated trophic cascades [14]. For instance, if areas of overlap are underused by neighbouring groups of a predatory species, that creates potential safer havens for their prey. Similarly, variation in space use could generate changes in the physical landscape, such as vegetation cover, by animals that act as 'ecosystem engineers' [104]; there could be both direct and indirect knock-on consequences for other species.

generates a heterogeneous 'landscape of intergroup conflict', in response to which social animals flexibly adjust their information gathering, space use, synchrony, signalling, and intragroup dynamics. These pre-emptive responses are shaped by multiple interacting factors and are mediated by the integration of sensed information with memories of past encounters. Just as the risk of predation can have a greater influence on prey than consumptive effects [13,101], the threat of intergroup conflict stands to have far wider-reaching consequences than the contests themselves (Box 3). Studying groups outside of direct contests—investigating how animals perceive, update, and make decisions about intergroup threat levels—will therefore reveal nuances in dynamic risk-limiting behaviour that affect many aspects of daily life, both for a given species and for those in its community (see Outstanding questions). To fully understand the influence and importance of intergroup conflict, including its role in our own evolution, we must study the complete timeline of behaviours—not just those during and after contests, but also those that occur in anticipation.

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Declaration of interests

The authors declare no competing interests.

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