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Review

Predicting the impacts of chemical pollutants on animal groups

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Chemical pollution is among the fastest-growing agents of global change. Synthetic chemicals with diverse modes-of-action are being detected in the tissues of wildlife and pervade entire food webs. Although such pollutants can elicit a range of sublethal effects on individual organisms, research on how chemical pollutants affect animal groups is severely lacking. Here we synthesise research from two related, but largely segregated fields – ecotoxicology and behavioural ecology – to examine pathways by which chemical contaminants could disrupt processes that govern the emergence, self-organisation, and collective function of animal groups. Our review provides a roadmap for prioritising the study of chemical pollutants within the context of sociality and highlights important methodological advancements for future research.

Highlights

Wildlife are exposed to an increasing number and diversity of chemical pollutants.

Chemical pollutants can elicit a range of sublethal effects on individual organisms, but research on how these contaminants affect social interactions and animal groups is severely lacking.

It is imperative that perspectives from behavioural ecology and ecotoxicology are integrated, to increase our understanding of how contaminant effects on individuals might cascade to group-level processes.

We present a conceptual framework for researchers and practitioners to guide the study of how chemical pollutants might affect the emergence, organisation, and function of animal social groups.

Chemical contaminants and animal sociality: a critical but neglected issue

Pollution arising from the production and consumption of synthetic chemicals now outpaces other environmental megatrends (e.g., rising CO_2 emissions [1]). Increasing human reliance, coupled with world population growth and insufficient regulation, has driven an exponential rise in the number of chemical products marketed globally (>350 000 [2]), and a corresponding surge in chemical contaminants infiltrating the environment [3]. Ecosystems worldwide are now exposed to a staggering array of compounds from agrochemicals [4] and metals [5], to pharmaceuticals [6] and personal care products [7]. Many pollutants degrade slowly and remain highly persistent in the environment, while others are released at a near-constant rate and are thus considered to be 'pseudo-persistent'. Consequently, chemical compounds have been detected in the tissues of a wide range of wildlife [8,9], pervading entire food webs [10,11].

A wealth of research dating back to Rachel Carson's seminal 1962 publication *Silent Spring* [12] has documented the adverse impacts of chemical pollution on wildlife. Besides causing mortality at acutely lethal levels, chemical pollutants can elicit a range of sublethal effects on animals, even at minute concentrations – including disrupting their behaviour. Such effects may be hidden drivers of population declines and ecological instability [13], fuelling calls for better integration of behavioural indicators into the environmental risk assessment of chemicals [14]. However, nearly all research in **behavioural ecotoxicology** (see Glossary) is focused on behaviours of individual animals, with little consideration for how chemicals might affect social interactions and emergent group functions. This is a critical oversight because many animals engage in social interactions over their lifetime and live within highly structured societies or form loosely structured **social groups** (Figure 1). These animals coordinate their behaviours with conspecifics to provide protection against predation, gain reproductive opportunities, find food, and reduce energy expenditure [15]. **Collective behaviour** thus directly affects both individual and group fitness.

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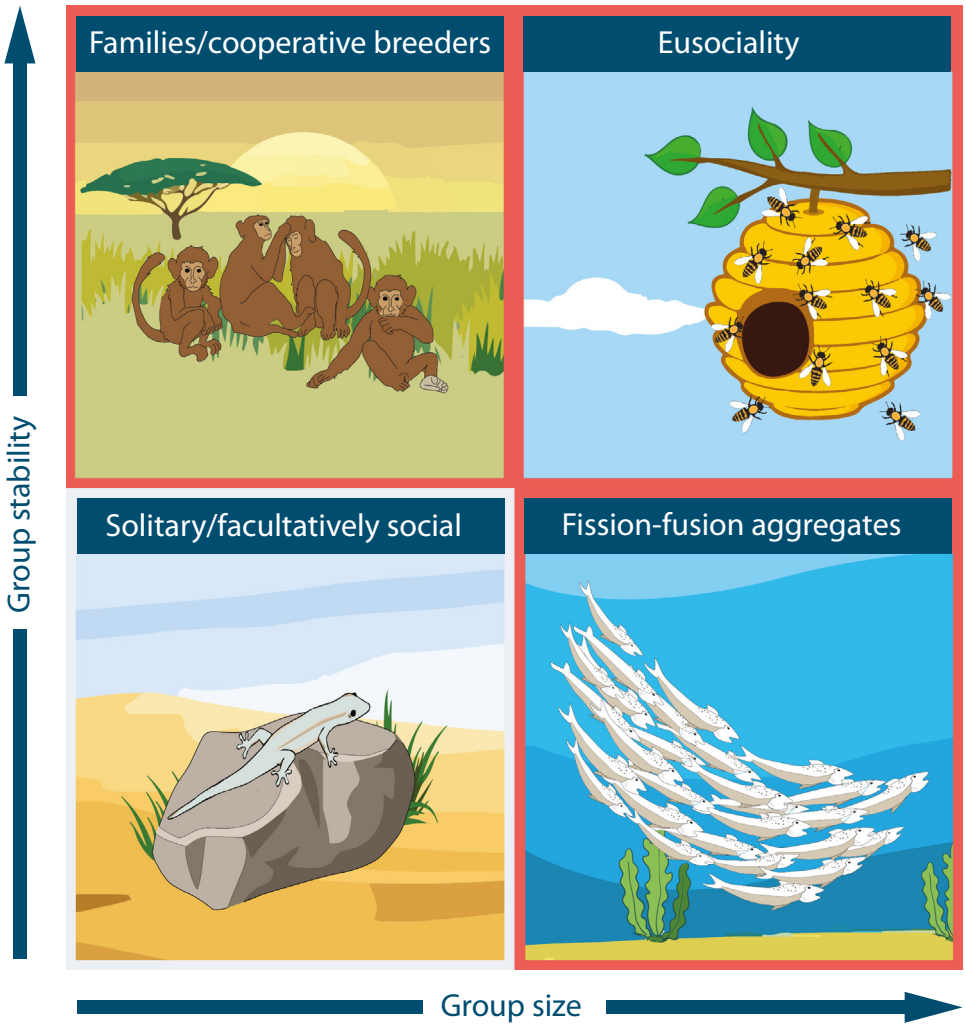


Figure 1. A general categorisation of social systems based on group size and stability, from mostly solitary species that interact occasionally with conspecifics (e.g., during the breeding season), to cooperative breeding groups and eusocial societies. While species are often broadly classified as living in groups or not, there is extensive variation among social species in the tendency to be social (e.g., facultative versus obligate sociality), typical group sizes, how stable group membership is over time, the extent to which individuals have consistent roles within groups, and the relatedness between individuals within a group. These variables can differ between populations of the same species, and social tendencies can differ among individuals within the same population. The red shaded region represents social systems where collective behaviour can emerge. Note that social complexity can also be arranged according to other group attributes including relatedness and reproductive skew.

Here, we present a novel framework that outlines how chemical contaminants could disrupt behavioural processes that are instrumental in the emergence and **self-organisation** of animal groups. We formulate predictions for how these disruptions may ultimately affect **collective outcomes**, detail how social behaviours themselves may exacerbate or buffer the effects of contamination, and provide a roadmap for prioritising which pollutants and species to research. Importantly, our review presents a timely opportunity to integrate key perspectives in behavioural ecology and ecotoxicology – a critical step towards improving predictions on the environmental threat posed by chemical contaminants [1].

Glossary

Anxiolytic: medications used to reduce anxiety and treat anxiety-related disorders.
Behavioural ecotoxicology: the study of animal behaviour to determine the potential impacts of chemical contaminants in the environment.
Collective behaviour: the coordinated actions of group members that emerge from local behavioural rules and social interactions, without central control.
Collective outcomes: the emergent properties of group actions. For example, coordinated movements, collective decision-making, and collective resource acquisition.
Endocrine disruptors: pollutants that mimic, block, or interfere with the endocrine system.
Fission–fusion society: the dynamic process in which groups change size and composition as they split (fission) and merge (fusion), for example, insect swarms, bird flocks, and ungulate herds.
Global scale: spatial and temporal processes that affect the formation of social groups and their corresponding traits (size and composition).
Local scale: spatial and temporal processes occurring within a group, such as interactions among group members.
Neural transmission: the process of communication between neurons in the brain. Pollutants can alter neural transmission by changing, mimicking, or blocking the molecular signals (i.e., neurotransmitters) and/or the signal receivers (i.e., neuroreceptors).
Phenotypic assortment: a process in which individuals are either actively or passively sorted into groups according to phenotypic traits (e.g., body size, colouration, habitat preferences, etc.).
Phenotypic composition: the different phenotypes that can be found in a group or population (e.g., diversity of body sizes, behaviours, or physiological attributes).
Self-organisation: the decentralised process of reaching group-level outcomes, which emerge from local interactions.
Social attraction: the tendency of individuals to approach and interact with conspecifics.
Social conformity: the process by which individuals within groups synchronise their phenotypes or shift their phenotype towards some group phenotype.

Predicting the impacts of chemical pollution on animal collectives: a conceptual framework

Chemical pollutants may influence collective behaviour by impacting the units that compose social groups (i.e., individuals) and/or the interactions among those units (i.e., sociality). Here, we detail how the effects of pollutants on individuals and their interactions can manifest across **local** and **global** spatial scales to change the formation and function of animal groups (Figure 2, Key figure). Our framework integrates behavioural and social mechanisms that underlie the formation and function of different types of social systems, from highly dynamic **fission–fusion societies** to relatively stable social groups.

Social competence: the capacity of an individual to adjust its behaviour to optimally match the current social context.
Social group: a collection of individuals that associate with one another, and typically have shared interests.
Social network: an analytical tool used to describe the social structure of groups, populations, and communities.

How do chemical pollutants impact individuals?

To predict how contaminants might affect animal social groups, we first need to understand how they can influence individuals at environmentally realistic exposure levels. Documented impacts range from mortality to severe physiological and physical impairment, to subtler effects that may not elicit a stress or escape response. Here, we focus on examples of sublethal effects that could have cascading implications at the collective level (Box 1).

Exposure to chemical pollutants can lead to dramatic morphological alterations, including changes to body size [16], colouration [17], and sex [18]. Perhaps most fundamental to animal social behaviour, pollutants can directly interfere with sensory anatomy involved in social communication (e.g., visual, auditory, olfactory, and tactile senses). Various compounds from surfactants to metals, pesticides, and herbicides can damage chemoreceptors and olfactory function in fish [19,20], amphibians [21], and insects [22], greatly reducing their ability to detect cues. In extreme cases, chemical exposure can even lead to the development of new sensory anatomy. For instance, female fathead minnows, *Pimephales promelas*, exposed to 17β-trenbolone developed nuptial tubercles, which are communication structures typically only found in males [23].

Beyond morphological abnormalities, exposure to chemical pollutants often causes physiological, neurological, and hormonal disruption, leading to changes in phenotypic expression [24–26]. For instance, pollutants can alter an individual's metabolic state, leading to increased foraging and activity [27]. Changes to neurological and cognitive function can occur when contaminants mimic or block the actions of neurotransmitters, neurohormones, or steroid hormones that modulate animal behaviour [28]. Chemical exposure can also disrupt neurological function by impacting the expression of key receptors for signalling molecules, the functionality of enzymes, or the modulation of **neural transmission** via de- or hyperpolarisation [29]. Pollutants stemming from human pharmaceutical medications, for instance, can alter wildlife behaviours, such as activity [30,31], risk-taking [30,32], and aggression [33,34], because these drugs target receptors that have been shown to be evolutionarily conserved across much of the animal kingdom [35].

Importantly, the effects of pollutants on individuals do not need to directly interfere with animal sociality to affect the formation and function of social groups. For instance, increased risk-taking in response to chemical exposure could alter the likelihood of an individual joining a group [36], or group cohesion [37] (Box 1). Ultimately, how chemical pollutants affect individuals, and groups, will depend on the chemicals' mode-of-action, and on the exposure concentration and duration. Some chemicals can affect behaviour at minute doses, while others require higher doses, and this depends on the chemical's structure, its intended (or unintended) biological target, and the sensitivity of the exposed species (Boxes 1 and 2).

Key figure

Framework for examining the impacts of chemical pollutants on social animals, from individuals to collectives

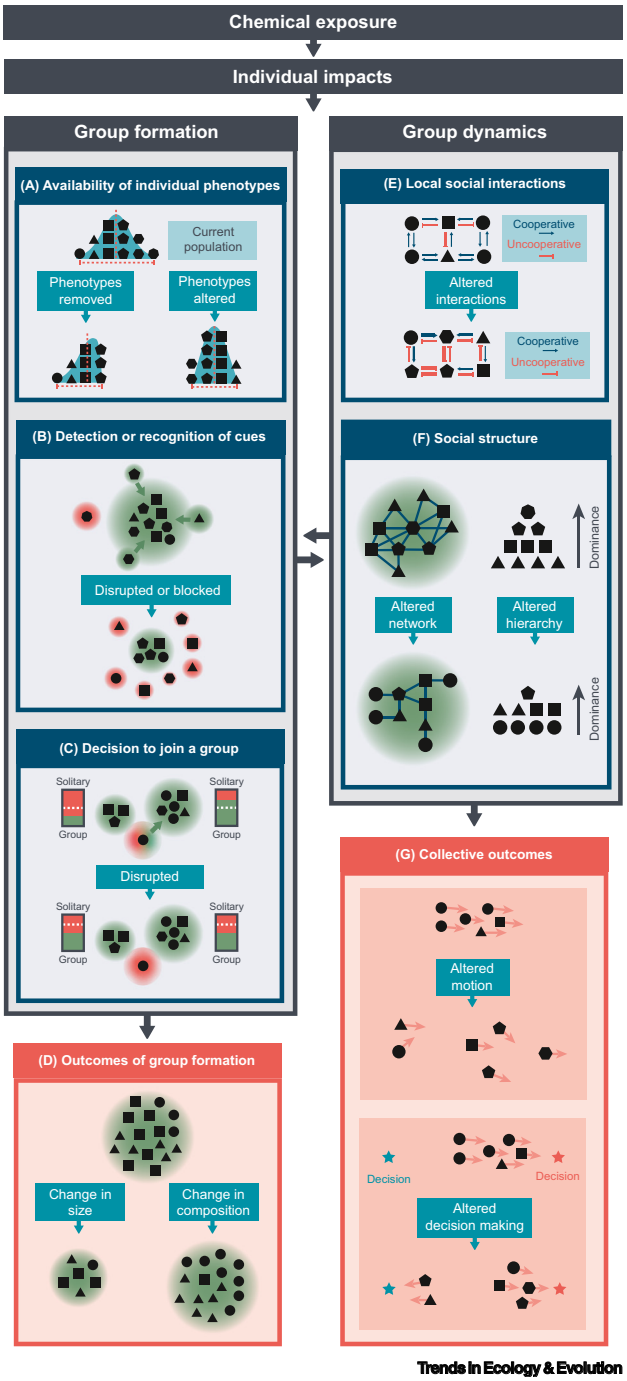


Figure 2. Chemical pollutants can fundamentally affect animal social groups by impacting the individuals (shapes in the figure) that comprise groups and their interactions. Effects on individuals can influence the formation of groups by changing (A) the availability of individuals (i.e., number of shapes) and phenotypes (i.e., different shape variants) within the current population, (B) the detection and recognition of social cues, as well as cue properties, used for attracting individuals to groups, and (C) the decision of individuals to join a group. Impacts on these processes will ultimately influence (D) the outcomes of group formation such as the number and phenotypic diversity of individuals within groups. Pollutants can also affect group dynamics by altering (E) social interactions among group members and (F) group social structure, which both (G) mediate collective outcomes. There could be feedback between the effect of chemical pollutants on group dynamics (E,F) and processes of group formation (A–C). While this framework focuses on within-generational effects, the described impacts could also persist across generations, causing evolutionary change.

Formation of groups

Social animals must form or join a group, and then maintain membership of this group over time. The need for spatial and temporal coordination is particularly acute in species with highly dynamic social systems like fission–fusion societies [38]. Changes in group size depend on the spatial and temporal availability of individuals, and the capacity of these individuals to detect, be attracted to, move towards one another, and maintain group cohesion. Here, we discuss how chemical pollutants can interfere with these key processes of group formation (Figure 2A–C).

Availability of individuals

Animal groups are composed of individuals that come from a population containing a variety of phenotypes. When chemical pollutants alter individual phenotypes, or directly remove individuals and phenotypes from the population, the number of individuals and the availability of phenotypes that can join a social group change (Figure 2A). Reduced population densities, for instance, may create a spatially segregated social environment with fewer conspecific encounters and interactions [39].

There are several ways in which chemical pollutants can impact the number of individuals and the availability of phenotypes for group formation. Pollutants can remove individuals from the population through mortality, or by causing physical impairment, which limits movement and thus the capacity to join groups. For example, birds that ingest lead from hunting ammunition fragments, or are exposed to oil spills and pesticides, can suffer hampered flight performance, movement, and metabolism [40–42], potentially impacting their ability to join flocks or collectively migrate [42].

Exposure to chemical pollutants can either homogenise (or diversify) phenotypic traits within a population by shifting individual traits towards (or away from) the population phenotypic mean, with potential downstream effects on the phenotypic variance of groups. For instance, exposure to fluoxetine (a common pharmaceutical pollutant), homogenised multiple behaviours in mosquitofish, *Gambusia holbrooki* [43]. Phenotype-dependent effects can also occur if the uptake of a chemical is phenotype-specific, or the chemical's mode-of-action is phenotype-specific [44]. Endocrine-disrupting chemicals, for instance, often cause sex-specific phenotypic effects [45], from behavioural changes to sex-reversal, potentially leading to sex-dependent recruitment rates, and consequently highly skewed sex ratios within groups.

Detection and recognition of social cues

For groups to form, individuals must locate suitable group mates using cues that include direct (e.g., visual, olfactory, or auditory) and indirect stimuli (e.g., scent markings or turbulence caused by the movement of conspecifics). Such cues act as forces of **social attraction** and facilitate group recruitment [46]. Chemical pollutants can interrupt mechanisms of attraction and recruitment by disrupting the ability of individuals to detect and recognise cues in the environment. Indeed, chemical agents are considered some of the worst environmental sensory disruptors [47].

Chemical pollutants can alter the properties of the cues themselves (e.g., their chemical composition) or the information they convey (Figure 2B). For instance, exposure to various agrochemicals changes the pheromone composition of honey bee queens, reducing their attractiveness to workers [48]. Further, chemical pollutants may indirectly alter environmental cues that animals use to aggregate. Group size, for instance, can itself be a cue for group formation [49]. A size threshold must often be reached in order for groups to stabilise or elicit a joining response [50]; thus if group recruitment is compromised by chemical pollution, initial group sizes may become too small to attract more conspecifics, leading to failed grouping attempts.

Box 1. Can we make generalised predictions for how certain chemical classes will impact animal groups?

Chemical pollutants present a unique challenge due to the sheer number of different chemical classes, and the existence of numerous modes-of-action between and within these classes. The effects of chemicals can be species-specific, and contingent on several factors, including the degree of homology between non-target species and the intended target species. Further, many classes of chemical pollutants do not have a primary mode-of-action that is conventionally associated with behavioural disruption (e.g., antibiotics, antihistamines), or are not specifically designed to elicit behavioural effects (e.g., metals, surfactants), yet can still do so. This makes generating generalised predictions for many chemical classes difficult. However, for chemical classes with designed biological targets, and documented pathways for behavioural disruption, general predictions may be valuable for directing future studies on their impacts on animal groups and sociality. In Table I, we outline a series of general predictions for how individual-level effects induced by contaminants are expected to have corresponding group-level consequences, and we identify chemical classes that are predicted to induce these effects.

Table I. General predictions for how individual-level effects induced by chemical pollutants could have corresponding group-level consequences

Individual-level effects	Chemical classes[a]	Group formation	Group dynamics	Refs
Antisocial behaviour	1,2,3,4,5	Reduced tendency to accept and form social groups. Higher rejection rate from potential group members.	Increased conflict amongst group members and weaker social networks. Altered social structure.	[33,34,92–94]
Reduced anxiety and risk perception	1,2,6	Decrease in the propensity of individuals to join groups (particularly if grouping is primarily an antipredator strategy).	Slow response times to group actions. Less group coordination and cohesion. Higher risk-taking and poorer predator evasion.	[30,57,93]
Hyperactivity	3,4	Higher social interaction rates, but lower capacity to adjust behaviour for group formation.	Faster group movement, altering group cohesion and polarisation. Hyperactive individuals may be rejected from unimpaired groups.	[95,96]
Lower activity/compromised locomotion	1,5,6,7,8	Inability for impaired individuals to join, or move between, groups.	Slower group movement, altering group cohesion. Impaired individuals likely rejected from groups.	[42,97–100]
Altered cognition	4,7,8	Reduced ability of impaired individuals to process social information including cues for group formation.	Reduced **social competence** and inappropriate responses to social partners. Poorer group decision-making and coordination.	[16,95,101]
Sensory disruption	3,8	Inability to attract and discriminate between potential group members. Reduced group assortment.	Poor communication between group members. Uncoordinated groups and increased failure rate of collective actions.	[20,23,60]

1-Antidepressants (e.g., selective serotonin reuptake inhibitors)
2- Anxiolytics (e.g., benzodiazepines)
3-Steroids (e.g., androgens)
4- Psychostimulants (e.g., central nervous system stimulants)
5- Analgesics (e.g., opioids)
6- Beta-blockers (e.g., nonselective blockers)
7- Anticonvulsants (e.g., dibenzazepines)
8- Insecticides (e.g., neonicotinoids)
[a]For each chemical class, we use an example chemical subgroup to narrow our predictions to specific biological targets. Chemical class and example chemical subgroup are 1–8.

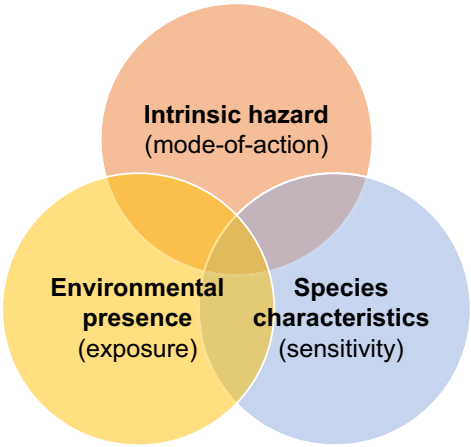
Contaminants can further interfere with the ability of individuals to detect cues. For example, parasitic wasps, *Nasonia vitripennis*, exposed to a neonicotinoid insecticide cannot detect pheromones to locate sexual partners [51], and juvenile rainbow trout, *Oncorhynchus mykiss*, exposed to copper-contaminated water during development are unable to detect conspecific alarm cues as adults [52]. Pollutants can also compromise cue recognition which enables individuals to discriminate amongst conspecifics and is a key mechanism for identifying suitable group members. Poor cue recognition could lead to a breakdown in communication among interacting individuals attempting to form or coordinate groups. For example, exposure to 4-nonylphenol (a common chemical constituent in detergents) reduces recognition of social cues in banded killifish, *Fundulus diaphanous*, leading to disruptions in shoal organisation [53].

Decision to join a group

Chemical exposure may alter the benefits received by individuals joining a group. While several studies have shown that exposure to chemicals can either attenuate (e.g., [54]) or intensify (e.g., [55]) individual preferences to join social situations the mechanisms underlying these

Box 2. How to best focus future research efforts

Numerous approaches are used for prioritising the scientific investigation and potential regulation of chemicals in the environment (reviewed in [102]). Most approaches first calculate a chemical's risk and then compare/rank risks among chemicals. Such risk calculations involve two main components: (i) identifying a chemical's intrinsic hazard and toxicity to organisms, and (ii) measuring its presence in the environment via monitoring studies, while also accounting for other factors that may influence its presence in the environment or exposure such as production volume or human use patterns [103]. In addition, (iii) species' characteristics and geographic distribution should also be considered when deciding research directions. Importantly, these components are not mutually exclusive, but interact. While ranking and prioritising chemicals is beyond the scope of this review, we can use these three key components to identify which chemicals and/or species we should focus research efforts on when studying the potential for contaminants to disrupt animal social groups (Figure I).



Intrinsic hazard (mode-of-action)	Environmental presence (exposure)	Species characteristics (sensitivity)
• Neurotransmitter or neurohormones that regulate social responses • Sensory/perceptual pathways important for social communication • Cognitive capacity to respond optimally to social cues • Motor or effector responses to perform behaviours • Morphological traits important for social grouping (e.g. sex)	• Exposure level and duration (e.g. detected more regularly or at higher concentrations in the environment) • Manufactured and/or used in high quantities • Persistent and bioaccumulate (i.e. not readily degraded or metabolized) • Pseudo-persistent (i.e. continuously added)	• Has physiological target/pathway that chemical can act upon (e.g. receptors, enzymes) • Depend on sociality for reproduction and survival (e.g. protection from predation) • Live in exposed environments with few options to disperse • Extent of individual and group-level plasticity (e.g. how social group respond to membership loss)

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Figure I. Venn diagram illustrating how three key components – intrinsic hazard, environmental persistence, and species characteristics – should be considered together when prioritising chemicals and species to be used to investigate potential impacts of chemical contaminants on animal groups. Further, the table below the diagram provides (nonexhaustive) examples of cases in which pollutants are most likely to affect social behaviour. Chemicals and species that sit at the intersection of these three components are very likely to affect social behaviour (the chemical perspective) or have their social behaviours affected (the species perspective).

changes are rarely elucidated. Individuals will typically aggregate if the benefits of grouping (e.g., safety in numbers) outweigh the costs (e.g., within-group competition). Pollutants may shift this cost–benefit trade-off, altering an individual's propensity to seek social opportunities (Figure 2C). Chemicals that impose higher physiological demands on organisms, for instance, may

decrease their propensity to join groups due to higher energetic costs of food competition [56]. Furthermore, chemical exposure may lead to maladaptive grouping decisions if the chemical induces phenotypic changes that are mismatched with the environment. For example, **anxiolytic** pollutants can alter the stress response of fish, lowering their perception of risk and decreasing their social tendencies, even when predation risk is high and being social is beneficial [57].

Chemical exposure that inhibits neural and cognitive function, including abilities to learn and perceive conspecific cues, can alter an individual's capacity to build social connections [58]. Individuals may prefer to group with similar phenotypes (i.e., **phenotypic assortment**), but if chemical contaminants compromise an animal's capacity to discriminate among phenotypes, individuals may exhibit reduced selectivity for groups and assort randomly or avoid grouping altogether. Although no studies have examined changes in the phenotypic grouping preferences of animals in response to chemical exposure, possible insights can be drawn from studies on the impact of chemical exposure on mating preferences (reviewed in [59]). For example, in female guppies, *Poecilia reticulata*, the preferences for male orange colouration (a signal of quality) is significantly reduced when females are exposed to the **endocrine disruptor** 17β-trenbolone [60], suggesting that females lose their ability to discriminate among male phenotypes.

Outcomes of group formation

By interfering with key mechanisms of group formation, chemical pollutants can change the size and **phenotypic composition** of groups (Figure 2D). Importantly, chemically induced changes to group formation may have broader implications for communities and ecosystem functioning if there is a population shift in the average number, size, and/or composition of groups. For example, lower group recruitment rates may lead to smaller average group sizes, which could, in turn, change consumer–resource dynamics that shape community trophic structures [61].

Group dynamics

Collective behaviour emerges from the social interactions and behavioural feedback among individuals that comprise a group. Therefore, chemically induced effects on individual behaviour, capacity to socially interact, or group composition may have far-reaching implications for collective outcomes.

Local interactions and social structure

Social interactions regulate the behaviours of group members, resulting in collective behaviours. For instance, individuals regulate their speed to match neighbouring individuals, resulting in coherent group movement [62]. Contaminants can alter local interactions either by compromising individual abilities to detect and process social cues or by promoting individual behaviours that increase or decrease social interaction rates within groups (Figure 2E). Changes in social interactions are expected to alter the emergence and coordination of collective outcomes. For example, exposure to oil pollution significantly impairs shoaling cohesion and alignment in Atlantic croaker, *Micropogonias undulatus* [63], and zebrafish, *Danio rerio* [64], even if just one group member is exposed [63]. By contrast, exposure to fluoxetine reduced swimming speed and aggression, promoting shoaling cohesion in Arabian killifish, *Aphanius dispar* [65].

Collective behaviour often relies on information transfer among individuals, which is influenced by the group's **social network**. Chemically induced aggression can lead to increased conflict among individuals (e.g., [34]), potentially leading to weaker affiliative connections and a disconnected social network [66]. By contrast, if contaminants act to either directly or indirectly increase an individual's social tendencies and increase social affiliations, network density and information transfer may increase [67]. The effects of chemical pollutants on within-group social

interactions will likely be more apparent if individuals who tend to have many social interactions are disproportionately affected, as these individuals can be essential for mediating information flow in the group [68]. Indeed, there is increasing evidence that dominant or highly interactive individuals may be disproportionately affected by certain chemical pollutants, thus changing group social structures [69].

Chemical pollutants can influence group composition by changing the phenotypes of individuals comprising the group (Figure 2F). The phenotypic composition of a group may dictate social structures such as dominance hierarchies and leadership, which can impact collective decision-making. For example, the boldest individual in a group typically initiates and directs collective movements [70,71]. By causing phenotypic changes, chemical contaminants may alter the number and/or identity of highly influential individuals (e.g., [65]). Various endocrine-disrupting chemicals, for instance, can decrease testosterone levels in fish, potentially promoting egalitarian social structures [72].

Variation within groups can often be important because of the synergistic collective outcomes that arise from interactions among different individuals [73]. For instance, in honey bee colonies, the proportion of scouts can determine collective foraging success in different environments [74] (Box 3). Therefore, chemically induced changes to group behavioural composition (e.g., [43]) may impact group dynamics and performance. For collective actions that require individuals to **socially conform** (e.g., collective motion during predator attacks [75]), pollutant-induced reductions in within-group heterogeneity may be beneficial for some group outcomes (e.g., cohesion). By contrast, in groups that divide labour or social roles, limited heterogeneity can disrupt task allocation and group functioning [76].

Collective outcomes

The effect of chemical pollutants on collective outcomes will depend on the pollutant and species in question (Boxes 1 and 2). Yet, in any context where group social structures or interactions are disrupted or modified, exposure to chemical pollutants is expected to alter collective decision-making, coordination, and overall performance of animal groups (Figure 2G). This will in turn impact how social groups respond to predator attacks [75], acquire and share resources [77] (Box 3), and sense changes in their environment [78]. Importantly, when collective actions fail, individuals will not reap the benefits of grouping [79], potentially leading to negative feedback and a higher probability of group fragmentation or colony failure [80].

Does living in social groups increase resistance, or sensitivity, to the effects of chemical pollution?

When considering the various pathways by which chemical exposure could impair group formation, composition, and emergent traits, an interesting question arises: are there also mechanisms by which sociality can dampen or amplify the effects of chemical pollutants?

First, sociality may modulate the effects of a chemical pollutant if the social structure leads to differences in pollutant exposure or uptake among individuals. For example, differences in metabolic rate or respiration associated with different social roles may lead to differential exposure via altered uptake and/or elimination of the compound [69]. Within a group, differential exposure could either ameliorate or exacerbate a pollutant's effect depending on the individual's role in the social group and the associated physiological phenotype of that role. Another means by which sociality may affect contaminant exposure is via social aggregation within polluted habitats. Social groups may attract unexposed individuals and increase their exposure in polluted microhabitats, creating a potential ecological trap. Individuals may then choose to stay in a polluted habitat if they can associate with conspecifics versus dispersing alone [81].

Box 3. A case study - honey bee collective foraging

Collective foraging of social insects emerges from interactions among individuals and the behavioural composition of a colony. A classic system for studying collective foraging is the honey bee, *Apis melifera* (Figure I). Because honey bees pollinate a wide range of crops, the use of chemicals, particularly insecticides, in agriculture has had a large impact on the health, behaviour, and survival of honey bees [26,104]. Exposure to insecticides can alter bee brain morphology and disrupt cognitive abilities [105], including learning [106], which can compromise the ability of bees to recognise colony members and food cues [107]. How these individual-level effects impact collective outcomes, however, is not well understood.

Honey bee foragers are recruited to food through an elaborate communication system in which returning foragers relay the direction and distance of food through dance [108]. The collective decision-making process that emerges from the ability of each bee to decipher the dance, requires substantial neurological activity [109]. Insecticide exposure could thus disrupt social communication between workers and foragers through effects on bee neurobiology. The impacts of insecticides on honey bee collective foraging may depend on the type of colony members exposed. For instance, honey bee foragers are more susceptible to pollutants because they regularly interact with the environment outside the nest compared with workers that primarily perform tasks inside the nest [110].

Honey bee workers differ in their ability to produce and follow the recruitment dance [74] and variation among colonies in the composition of different phenotypes can influence how colonies collectively acquire different foods [111]. These differences may impact colonies' exposure to pollutants and therefore result in differential impacts of insecticides on collective foraging. First, individual differences in foraging decisions, including where bees choose to forage, may result in variation in the pollutants to which each individual is exposed. Second, because individuals differ in their learning capacity, and therefore foraging decisions, there may be differences in how each individual and each colony are impacted by chemical pollutants. Depending on how a pollutant impacts the neurological pathways that underlie learning and communication, some individuals and colonies may be more strongly impacted than others. Such differences in how pollutants impact both individuals and colonies may then have downstream effects on where honey bees forage and which crops they pollinate. Potential feedback between variation in exposure to pollutants and differential impacts on collective foraging may result in substantial ecological and economic impacts.

Figure I. (A) A single honey bee forager on a flower, (B) honey bee foragers returning to the hive, and (C) honey bees interacting on a comb inside the hive. Photo credits from left to right: Noa Pinter-Wollman; iStock.com/bo1982; iStock.com/temmuzcan.

The second way in which sociality may ameliorate or exacerbate pollutant-induced effects is if the social structure itself modulates the impact of the pollutant. For instance, the expression of certain phenotypes, like behaviour, may be constrained as individuals conform to the group or to their roles within the group [82] (e.g., a reduced movement range, suppressed reproduction). In such cases, grouping may reduce the phenotypic space in which a contaminant can operate, and thus reduce the observable impacts of the chemical. For example, contaminants that disrupt reproductive behaviour may have little impact on an individual that is reproductively suppressed. By contrast, if a chemical affects phenotypes that are critical for maintaining group structure, then that chemical's impacts will likely be greatest in a social setting. For example, if chemical exposure increases aggression, it may have a larger impact on societies where dominance hierarchies are important.

Finally, sociality can buffer individual stress responses (e.g., by reducing cortisol in mammals: [83], and fish: [84]). Therefore, chemical pollutants that increase stress may be buffered by

group living. However, whether social buffering changes pollutant uptake or the phenotypic space upon which the pollutant acts will require further investigation. It will also depend on the organism's social structure and how that social structure affects their physiology, behaviour, and interactions with other species in the ecosystem (Box 2).

Approaches for exploring the impacts of chemical pollutants on animal sociality

Research on the impacts of chemical pollutants on collective behaviour, and animal sociality more generally, is extremely limited. Progress in this area clearly requires improved collaboration between researchers in behavioural ecology and ecotoxicology, and better integration of experimental approaches across these fields. For instance, behavioural ecology has long-recognised the importance of the social environment in mediating the behavioural expression of individuals, yet the standard experimental approach in behavioural ecotoxicology is to test the behaviour of individuals in isolation, ignoring the social environment altogether [85]. On the flipside, limited knowledge of chemical exposure protocols and pollutant prioritisation (Boxes 1 and 2), as well as limited access to specialised analytical technology, are likely key impediments for many behavioural ecologists interested in studying the effects of chemical contaminants on social behaviour.

Despite these roadblocks, there has never been a better time to explore the potential effects of chemical pollution on animal collectives. Under laboratory conditions, collective behaviour can be quantified using consumer-grade video cameras and freely available software (e.g., [86]). Improvements in remote-sensing technologies, such as global positioning system (GPS) and acoustic telemetry, and associated quantitative tools (e.g., social network theory), now also make it possible to study the potential effects of chemical contaminants on collective behaviours in the wild, including large-scale movement events (e.g., migration) [87]. These methods have already been utilised to study the impacts of agrochemicals on social insect colonies, which provide some of the best, and so far only, examples of how contaminant effects on individuals can scale up to impact group performance (e.g., [76,80]; Box 3). A particularly exciting new experimental approach is to combine biologging technology with targeted exposure devices (e.g., slow-release exposure implants; [88]) that isolate chemical exposure to specific individuals, allowing for the direct quantification of chemically induced behavioural effects in nature, as well as the flexibility to study both control and exposed organisms in the same natural system. The aforementioned automated approaches provide near-continuous sampling of individual behaviours and social interactions providing unparalleled opportunities to not only understand how contaminants affect social groups, but also how changes in social connections and structures in response to chemical exposures can affect related ecological phenomena (e.g., cultural transmission) [89,90].

Concluding remarks

Behavioural ecotoxicology has provided important insights into how chemical contaminants impact individual organisms. However, given the fundamental role that social and collective behaviours play in animal fitness and population stability, it is imperative that we bridge approaches in behavioural ecology and ecotoxicology to better understand how pollutant-induced effects on individuals might cascade to group-level processes (see Outstanding questions). Integrating collective behaviour into ecotoxicity studies is particularly important in light of recent evidence that behavioural endpoints are largely ignored in chemical risk assessments when not linked to population or higher-order ecological outcomes [91]. Thus, our framework provides an important guide for researchers and practitioners to predict how chemical stressors will likely affect the emergence, organisation, and function of animal social groups.

Outstanding questions

What are the mechanisms and pathways by which different chemical pollutants (and their mixtures) affect individual sociality?

How do contaminant-induced changes in population phenotypic composition affect the formation and properties of animal groups?

Can exposure to chemical contaminants disrupt grouping decisions and preferences?

How do contaminant-induced behavioural changes at the individual level affect the structure and social network of animal groups?

Does exposure to chemical contaminants lead to higher group fragmentation or poorer collective outcomes (e.g., slower decision-making)?

Does animal sociality exacerbate or ameliorate the effects of chemical pollutants?

Do different forms of sociality (e.g., facultative versus obligate social systems) differ in their vulnerability to chemical pollutants?

How do contaminant-induced changes at the collective level (if observed) affect broader ecological phenomena (e.g., population dynamics, migration, disease transmission)?

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Declaration of interests

The authors declare no conflicts of interest.

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