

Interspecific information transfer influences animal community structure

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Acquiring information from the cues and signals of other species of the same trophic level is widespread among animals, and can help individuals exploit resources and avoid predators. But can such interspecific information transfer also influence the spatial structure of species within communities? Whereas some species use heterospecific information without changing their position, we review research that indicates that heterospecific information is a driving factor in the formation or maintenance of temporary or stable mixed-species groups. Heterospecific information can also influence the organization of such groups, including leadership. Further, animals sometimes select habitats using heterospecific information. We survey interspecific information transfer, and evaluate the morphological, ecological and behavioral factors that make some species information sources and others information seekers.

From the transfer of genetic information between generations on an evolutionary timescale, to the acquisition of environmental information on an ecological timescale, information underlies life. At the ecological timescale, animals have a basic choice: they can acquire information about resources and predators themselves, or they can gather such information indirectly from other individuals [1]. Although much information is acquired from members of the same species, information can also be gathered from individuals of other species ('heterospecifics'), and might be particularly valuable from heterospecifics of the same trophic level, because these species often require similar resources and need to avoid similar predators. The cues and signals produced by other species are part of the 'public information' available to many animals, through which animals are able to assess habitat, the presence of resources or potential risks [2,3].

Interspecific information flow has been the focus of much research recently, particularly because it has been found that heterospecific signals can be highly informative, for example about predator type [4] or level of risk [5–7]. Indeed, in a provocative review, Seppänen et al. [8] proposed that if the information from heterospecifics is similar

to that from conspecifics, information from heterospecifics could be more valuable, because heterospecifics might impose less competitive cost at close distances than conspecifics. There is a tradeoff here: the closer the two species' ecological niches, the more relevant their information to each other, but the greater the competition, too. Consider, however, two species that differ in their foraging niches, and hence are quite tolerant of each other's presence, yet are of the same size and are preyed upon by the same predator: such species might be highly useful to each other as sources of information about threats.

A neglected question arising from this work is whether interspecific information transfer is an important factor in the structure or assembly of communities (*sensu* [9]). Here we examine specifically the consequence of information transferred among species at the same trophic level on the formation of mixed-species groups, which we define broadly as any clustering or aggregation of individuals of different species in space or time. We do not discuss information transfer between species from different trophic levels, such as predator–prey [10] or parasite–host relationships, as we see for the most part such information

Glossary

Community: The set of organisms that exist in a spatially and temporally defined area.

Cue: The presence or behavior of an animal that can provide information to another animal, but has not evolved specifically to provide information to that animal (see contrast to 'signal', below).

Eavesdropping: The use of a signal by an animal that was not the intended receiver.

Information: Data that, when acquired, reduces an animal's uncertainty about environmental or social conditions, and that can be used by the animal to increase its fitness.

Intended receiver: An animal whose receipt of signal information benefits the information producer.

Mixed-species group: Any spatiotemporal clustering of individual animals of at least two different species.

Public information: Cues or signals produced by an animal that can be used by other animals to assess environmental conditions.

Signal: A feature or behavior of an animal (the 'signaler') that has evolved specifically to provide information. Such information benefits the signaler by producing an advantageous response in another animal (the 'intended receiver').

Trophic level: The position an organism occupies in a food chain, determined by what it consumes, and what consumes it, classified broadly.

Value of information: The difference in fitness of an animal caused by the acquisition of information.

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flow mediating interactions that are already occurring, and producing few reverberations among other species. Likewise, information transfer is important in the maintenance of pairs of mutualists [11], but we do not focus on such interactions because the direct benefits (nutrition, defense) often appear to outweigh information benefits.

Mixed-species groups provide tractable models for broader questions in community ecology, such as predicting patterns of interaction among species (Box 1). Yet, with a few exceptions (e.g. see Ref. [12]), the literature on such groups tends to be dispersed across taxon-specific publications. We attempt here to survey this literature, and to recognize the overarching theme of information use in shaping the structure of mixed-species groups. We begin by describing the influence of interspecific information transfer on the spatio-temporal distribution of species, and then assess the morphological, ecological or behavioral factors that can produce differences among species in the information that they make available to other species. Note that by the phrase ‘make available’ we do not mean to imply that the animals intentionally provide the information: information can be provided unintentionally from the simple presence of an animal, in the cues that it provides through its behavior to other animals, or in signals that have specifically evolved to encode information to conspecifics or heterospecifics [13].

The role of interspecific information in mixed-species groups

Interspecific information can have varying effects on community structure. Interspecific information can have no effect whatsoever, be a driving factor in temporary associations, or form the basis of associations between species that live together for most of their lives (Figure 1).

No effect on grouping

Some heterospecific information can increase the fitness of animals yet have little effect on the spatial position of individuals of different species relative to each other (Figure 1a). These situations often involve eavesdropping on information about predators provided in alarm calls, which warn of immediate danger from a predator and cause individuals to freeze or flee to cover [14]. Many vertebrates respond to the alarm calls of other species that have the same predators but with which they do not form groups [15,16]. For example, the Galapagos iguana (*Amblyrhynchus cristatus*) responds to alarm calls given by Galapagos mockingbirds (*Nesomimus parvulus*) despite having no association with the birds other than living in the same habitat [17]. Terrestrial organisms often eavesdrop on acoustic signals, whereas aquatic organisms, some terrestrial amphibians, and some insects use olfactory alarm information, such as that elicited by prey being attacked by a predator or the chemicals released by a damaged or dead animal [18–20]. In these examples, the animals might move towards refugia in directions independent of the source of information, or might scatter away from the area of attack; regardless, long-term movements are not affected.

Temporary groups

Some information about predators concerns an on-going threat, rather than imminent danger, and can result in

Box 1. Mixed-species groups as models for community ecology.

Community ecology often defines the community as all of the organisms living in an area [9], and mixed-species groups, which represent subunits of the full community, have not typically been a focus of the field. However, the large questions of community ecology are applicable to mixed-species groups: are such associations just random sub-samples of the community or are they structured by interspecific interactions [80,81]? In fact, mixed-species groups can be particularly good models for community ecology for two reasons. First, given a reasonable definition of what a mixed-species group is in the field (i.e. what is the maximum distance between members of different species and how long does an individual have to remain with the group?), any member of the overall community can be classified unambiguously as either inside the mixed-species group or not. Second, mixed-species systems can be found throughout the world, which offers an opportunity to look for universal patterns among communities that have different evolutionary histories [34]. The overall objective of research in mixed-species groups is clear: given a list of species in an area, and some selected morphological, ecological or behavioral characteristics of those species, researchers should be able to predict which species interact together in mixed-species groups (Figure 1).

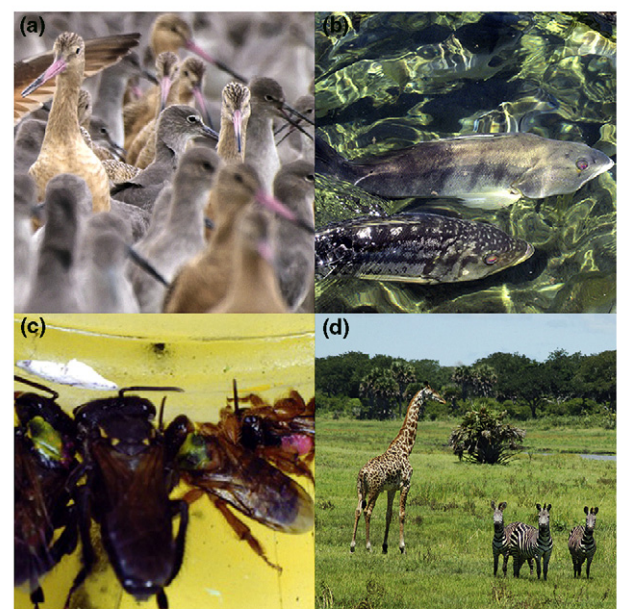


Figure 1. Examples of mixed-species groups. (a) Mixed flock of willets (*Catoptrophorus semipalmatus*) and marbled godwits (*Limosa fedoa*) in a marsh in western U.S.A. Photo credit: Ingrid Taylor. (b) Mixed school of fish in saltwater lagoon in western U.S.A. Top: sand bass (*Paralabrax nebulifer*), bottom: kelp bass (*Paralabrax clathratus*). Photo credit: Raphael Mazon. (c) Several species of stingless bees foraging at an artificial feeder in Panama. From left to right: *Partamona peckolti*, *Scaptotrigona barrocadoensis*, and *Plebia franki*. Photo credit: James C. Nieh. (d) Giraffe (*Giraffa camelopardalis*) and Burchell's zebra (*Equus burchelli*) group together on a floodplain in Tanzania. Photo credit: Tim Caro.

temporary associations among species. For example, animals produce mobbing calls upon detecting a predator not posing immediate danger [14], and these attract both conspecifics and heterospecifics. The calls therefore result in temporary mixed-species groups that monitor and harass the predator (Figure 1b [14,21]). Heterospecific mobbing is mainly described in birds, but can also occur in other vertebrates, such as among primates [22]. Mobbing groups do not appear to be chance subsets of the species in an area, without any organization; rather, which species

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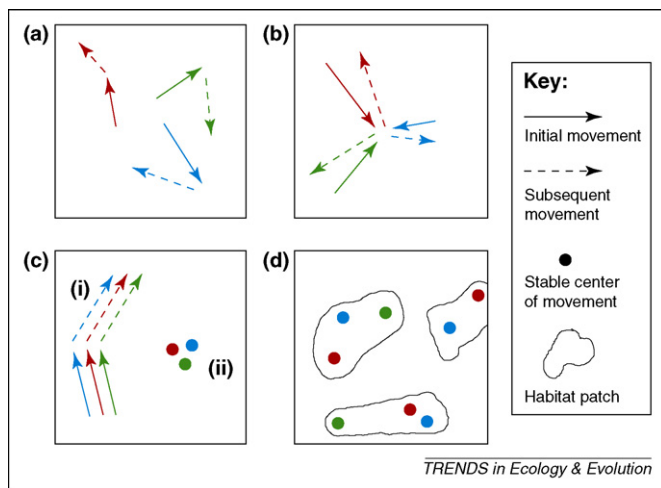


Figure 1. Different kinds of movement and spatial patterns among species, with different species being represented by different colors. ‘Initial movement’ is movement in response to acquisition of information from another species, whereas ‘subsequent movement’ is movement after the initial response. (a) In some instances, such as response to heterospecific alarm, initial movements towards refugia might appear random, or movement might be away from the place of attack; later movements are not affected. Solid arrows indicate initial movement and dashed arrows indicate subsequent movement. (b) Temporary groups among species occur around predators (‘mobbing’) or around food sources; information transfer can be vital in forming or maintaining such groups. (c) Stable mixed-species groups can either be (i) roving groups or (ii) mixed-species nesting or roosting colonies. Information transfer among species plays a role both in the composition of these groups and their organization. Dots represent a stable center of movement. (d) Species can select appropriate habitat by cueing in on the presence or behavior of heterospecifics, a phenomenon known as ‘heterospecific attraction’. Enclosed areas represent habitat patches. In both (b) and (d), information transfer can result in mixed-species grouping or dispersion (see main text).

join and initiate mobbing might be related to the vulnerability of the species to predation [21,23]. Thus, interspecific information influences the organization as well as the presence of mixed-species groups, a theme we will return to in discussing stable mixed-species groups as well.

Information about resources will often last longer than that about predators, and species can use such resource information to adjust their location, either by aggregating at resources or avoiding locations where resources have been depleted. One of the central models for studying such behavior is pollinating insects, which can use the sight or smell of other insect species to find rich food sources or to avoid flowers that have been visited [24–26]. For example, the sweat bee *Halictus aerarius* can avoid flowers depleted of nectar by recognizing and avoiding the olfactory cues left by either conspecific or heterospecific bees that have already collected from these flowers [27]. When insects are attracted towards other species, one result can be multi-species groups (Figure 1b [28]). Another outcome is that a dominant species usurps the resources of other species: for example, the stingless bee *Trigona spinipes* can eavesdrop on olfactory marks that a subordinate species has placed on rich resources and then dominates the resources, excluding other species [29].

Temporary mixed-species groups connected to resources are widespread among taxa. In addition to pollinating insects, mixed-species groups have been reported in reptiles that gain cues from birds [30] and ants that share odor trails with heterospecifics [31]. In birds, research has focused on species that feed on carrion [32] or schools of

fish [33]. In these groups, aggressive, dominant or klepto-parasitic species often gain cues from the presence of subordinates [32,33], in a similar manner to the example of stingless bees above.

Stable groups

In contrast to temporary groups, many species form stable mixed-species groups that persist regardless of the temporary distribution of threats or resources (Figure 1c). Such groups are found in birds [34], fish [35], insects [31], and mammals [36]. Mixed-taxa groups can be found as well, such as groups of hornbills and mongooses in Africa [37]. Such stable groups can be mobile (e.g. flocks or herds), or can stay in one place (e.g. colonies or roosts). There are several potential information benefits to joining mixed-species groups (Box 2). In brief, mixed-species groups can provide information but with lower competition for resources than experienced within single-species groups, and different species can produce information with different characteristics leading to an accumulation of information in a mixed-species group. In addition, different species can increase the overall group size, or grouping between species that are similar in their appearance can enhance the effectiveness of anti-predator behavior.

Box 2. Benefits to individuals in mixed-species groups.

One of the primary benefits to mixed-species, as opposed to single-species, groups is that because different species have different niches, individuals might gain group benefits with less competition [82]. So if heterospecifics can give some of the information benefits that conspecifics can give (for example, information about predation available in calls of frogs [83]) individuals might prefer mixed-species groups over single species ones.

A second argument for mixed-species groups is that the different species can detect information in different ways, and therefore the sum of information in a mixed-species group could make individuals more aware of environmental conditions than they would be in a single-species group. For example, different species in a mixed-species flock of birds can inhabit different layers of a forest, and therefore be aware of different kinds of threats [84], or species can differ in the information content of their signals [73]. Mixed-species groups can also allow larger groups (and consequently higher vigilance) than conspecific groups, as conspecific group size can be constrained by social factors such as territoriality [85] or low abundance [86].

A different set of hypotheses relating interspecific information transfer to mixed-species entails groups forming from species that resemble each other. Such groups have been reported in birds [87] and in fish [88]. Two potential reasons for such associations involve interspecific information transfer. First, if all the species share the same signaling mechanisms (due to shared ancestry, as has been suggested for alarm chemicals in fish [89], or convergent evolution, as has been suggested for the alarm calls of birds [90]) they can communicate in the same way as do conspecifics, although the mixed-species group can allow larger group size. Second, information transfer in this case might be aimed at a receiver at another trophic level, the predator. Predators might be better able to detect and attack animals that do not look like the others in a group (a phenomenon known as the ‘oddity effect’ [91], but see Ref. [88]). Alternatively, some or all species in the group might be distasteful or toxic, while others employ Batesian or Müllerian mimicry to avoid predators [92].

In the hypotheses above, all the different species in the flock are treated equally. Species differ, however, in their information-producing capacity which can lead to species that are poor information detectors following species that are good information producers.

Many of the examples in [Box 2](#) relate to information about predation; the evidence for the transfer of information about resources in mixed-species groups is more limited. A famous attempt to link the existence of mixed-species groups to information was made by Ward and Zahavi [38], who proposed that colonies or roosts of birds, both single species and mixed species, could serve as ‘information centres’ to locate clumped food patches. Specific support for their argument has proven evasive [39], and for mixed-species bird flocks, information about food resources can only be useful if the species have similar niches and foraging techniques, a situation that occurs most frequently if species are closely related or morphologically similar [40,41]. Learning about resources from heterospecifics has been reported, however, for mixed-species shoals of fish [42,43].

Most of the adaptive hypotheses for the formation of stable mixed-species groups presented in [Box 2](#) assume all species contribute information equally, but such groups can also result from asymmetric information transfer, particularly about predation risk.

Asymmetric information transfer can influence the organization of the groups, including which species lead groups or initiate their formation and which species follow or join groups. A common pattern is for less vigilant species to follow or join more vigilant ones and eavesdrop on their alarm calls. Many examples of such relationships come from studies of birds in mixed-species nesting colonies [44] or mixed-species flocks [45–47], but similar patterns can be found in mixed-groups of mammals such as ungulates and primates [48,49].

In groups with asymmetric information transfer, the joining species can be commensal or even parasitic on the information-providing species; for example, woodpeckers and nuthatches often follow chickadees in North America, listening to the chickadees’ alarm notes, and sometimes supplanting the subordinate chickadees at food sources [45,50]. However, relationships can be mutualistic if the joining species provides a different type of benefit than information. For example, hornbills give alarm calls that inform mongooses of predators, whereas the mongooses disturb (‘flush’) insects into the open, allowing the birds to eat them. Similarly, gobies provide tactile information about predators to alpheid shrimps, which dig the burrows in which they live [51].

Stable geographic distribution

Until now, we have been discussing the spatial position of animals relative to each other within habitats. At a larger geographic spatial scale, interspecific information can be important in habitat selection ([Figure 1d](#)). Migrating species can choose where to settle based on the presence of other species that share their habitat requirements, a pattern that occurs in both amphibians [52,53] and birds [54,55]. Animals can choose to settle near other species (‘heterospecific attraction’), but can also be repelled by dominant heterospecifics [56]. Animals can also gather cues of the reproductive success or behavior of other species as well as of their presence [57]. A fascinating example is that of red-backed shrikes (*Lanius collurio*) that use larders of impaled prey made by great grey shrikes (*Lanius*

excubitor) to choose where to settle [58]. One might expect that species that overlap in their habitat requirements would be equally good sources of information to each other. However, there could also be asymmetric transfer of information if some species are better or faster at assessing resources (a simple example would be a species that is already present in a habitat when another species arrives [54]).

Differences among species in information provided to heterospecifics

Although mixed-species associations can occur among species that have the same information-generating capacities ([Box 2](#)), many groups also occur between species producing information and species seeking that information (for example, where non-vigilant animals follow vigilant ones). Here we consider what morphological, ecological or behavioral factors can underlie differences among species in the information available to heterospecifics.

The provision of useful information to another species requires that: (1) an animal gathers information about the environment, (2) it produces information either as a cue or as a signal, and (3) the information is acquired by another species ([Table 1](#) [59]). For example, an individual might (1) detect a predator, (2) flee noisily from that predator (like the ‘wing-whistle’ of fleeing crested pigeons, *Ocyphaps lophotes* [60]), or make an alarm call, and so (3) alert heterospecifics. Species can vary in the acuity and accuracy with which they gather information, the proportion of information gathered that is converted into signals or cues, and the efficiency with which these signals or cues are detected by other species. There can be differences among species at each stage. We provide detailed information and examples in [Box 3](#), but here focus on two issues related to how information accuracy and value can differ between stages.

First, the accuracy of information available to a heterospecific depends on both the information gathering and production stage. Species can differ in the percentage of detections they make that are false, such as when individuals give ‘false alarms’ to harmless stimuli that they mistake as threatening [16,61]. Animals can also differ in the percentage of signals that are not prompted by a perceived threat, such as when individuals give ‘false alarms’ to manipulate other species [62–64]. In the first instance information is inaccurately gathered, whereas in the second it is inaccurately produced.

Second, the value of the information (*sensu* [65]) can differ at two different steps in the process. The value of the information gathered directly from the environment can vary among species: those that have a particularly strong need for a resource or are highly vulnerable to a particular threat might expend more energy in detecting it. For example, birds that build vulnerable open-cup nests can be particularly strong mobbers [66]. The value of the information can also vary for heterospecific receivers; some classes of information, such as alarm calls, might have larger effects on heterospecific receivers’ fitness than other classes of information. The value of the information to the receiver also depends on the overlap between the stimuli of

Table 1. Interspecific information transfer outlined as a three-step process: information detection, information production, and information transmission. Qualities of the information provided by the information producer are shown for each step of this process: a plus [+] sign indicates that enhancement of that quality results in enhancement of information transfer. The morphological, ecological or behavioral attributes of the information producing species that underlie difference in information detection, production and transmission are also shown (see also Box 3). Plus signs [+] indicate that an enhancement of that attribute improves the quality of the information, whereas minus signs [–] decrease the quality; [+/-] indicates situations in which either could occur.

	Stage of interspecific information transfer		
	Detection by information producer	Production by information producer	Detection by heterospecific receiver
Qualities of information	1. Sensitivity of detection [+] (% of stimuli detected) 2. Accuracy of detection [+] (% of detections that were associated with actual stimuli) 3. Value of information for the information producer [+]	1. Propensity to produce information [+] (% of detections turned into information) 2. Accuracy of production [+] (% of information produced that was stimulated by a detection)	1. Propagation of information [+] (% of information detected by heterospecific receivers) 2. Value of information for the heterospecific receiver [+]
Morphological, ecological, or behavioral attributes of information producing species that influence the quality of the information	1. General morphology [+/-] 2. Sensory physiology [+/-] 3. Foraging ecology [+/-] 4. Number of individuals [+]	1. Conspecific audience [+]	1. Conspicuousness [+] 2. Dominance [–]

importance to the receiver and the stimuli of importance to the information-generating species. Receivers should only value those signals or cues that encode information about stimuli of importance to themselves [16].

A final issue in discussing information asymmetries is whether the relationship between information producers and heterospecific receivers is analogous to that between producers (P), who find resources themselves, and scroungers (S), who cue off producers, in P-S models (e.g. see Ref. [67]). Multispecies groups break the fundamental assumptions of P-S models in that group members are probably not able to choose between tactics: species are likely constrained by their morphology, ecology and behavior to produce information of a certain quality (see Table 1). However, the relative quality of the species' information production, compared to other species, could change depending on the composition of the group that individuals of that species participate in. This possibility emphasizes the importance of dominance: dominant species might be able to select mixed-species groups in which they can act as information seekers, whereas subordinate species might be trapped in producing roles.

Testable hypotheses related to interspecific information transfer

The differences among species in information gathering, production and transmission suggest some simple, testable hypotheses. For example, in Box 3 we argue that the conspecific audience of an information-producing species affects the production stage of interspecific information transfer, that its conspicuousness affects the transmission stage, and that the overlap between the niches of the information producer and the heterospecific receiver affects the value of information for the receiver. Given these effects, generalist species that live in large, kin-structured conspecific groups should be the most attractive information providers to a wide range of other species.

Another class of testable hypotheses is related to whether the information producer benefits from the heterospecific audience or not. We hypothesize that species

that suffer a cost from their associates, such as subordinate species subject to parasitism by dominants, should reduce the conspicuousness of their signals, with the limitation that the signals still be effective to conspecifics. For example, a specific hypothesis that requires testing is that olfactory eavesdropping on odor trails might have led bee species to evolve less conspicuous mechanisms of finding resources, such as odor marking the food source only, or even limiting communication to inside the nest [29,68]. By contrast, if information producers benefit from their associates, they should increase the conspicuousness of their signals, and preferentially use them when a heterospecific audience is present. Potential examples of this last hypothesis include drongos (Dicruridae), a particularly vocal family of birds that usually associate with other animals and benefit by foraging on flushed insects. They have been observed to make more alarm calls when other species are present [63], and to imitate other species, attracting heterospecifics towards them [69].

In addition to variation among species in production of information, it is important to consider variation among heterospecific receivers of that information: under what circumstances does a species decide to detect resources itself as opposed to using heterospecific information? We hypothesize that socially subordinate species should invest more energy into acquisition of information directly from the environment, or invest in the sensory machinery to do so, whereas dominant species should invest more in seeking cues or eavesdropping on the signals of heterospecifics. A related question is whether one can classify species by their reliance on heterospecific information. It might be possible to distinguish between heterospecific information use that is opportunistic (i.e. any individual or species can in theory obtain the information, but it is just a matter of which individual is at the right place at the right time), biased (i.e. some species are better at providing certain types of information than others) and obligatory (i.e. there is no other way to obtain the information except from heterospecifics). This last obligatory class of heterospecific receivers appears to be rare [70], with the only example we

Box 3. Morphological, ecological and behavioral factors that affect information provision to heterospecifics.

Species can differ from each other in a number of morphological, ecological, and behavioral ways that produce variation in the amount and quality of the information they provide to heterospecifics. Differences relate to information detection, production or transmission (see also Table 1).

Information detection:

- General morphology. The overall body plan of a species can lead to superior resource or predator detection. For example, the ability to fly allows birds to find patchily distributed food faster than lizards [30].
- Sensory physiology. Some species are better at detecting resources or threats than others. For example, turkey vultures (*Cathartes aura*) search by smell and usually find resources more quickly than visually searching black vultures (*Coragyps atratus*), which instead take cues from the turkey vultures [32].
- Foraging ecology. The spatial position of a species or its foraging technique can affect resource or predator detection. For example, birds that catch insects in the air are constantly scanning and more likely to detect predators [62,73].
- Number of individuals. Species with larger group sizes will be more likely to rapidly detect predators [14], patchily distributed food resources [93], or nest sites [94]. Leader species of mixed-species flocks tend to be gregarious [95] and large colonies of stingless bees can quickly find food sources [96].

Information production:

- Conspecific audience. Species will be strong information producers if they have an important conspecific audience: kin or mates [97] or familiar individuals that reciprocate [98]. This could explain why leading species in mixed-species flocks of birds are not only gregarious but also tend to be cooperative breeders [34] or why most species that make alarm calls are social [15].

Information transmittance:

- Conspicuousness. Conspicuous species can be detected at long range. For example, the presence of albatrosses serves as a good indication of fish [99]. Similarly, the loud calls of a tanager can be used by other species to find fruit [100].
- Dominance. While dominant species can use subordinate species to find and exploit food locations, the opposite is often not true. Dominant species of stingless bees have been shown to use the presence or chemical cues of subordinate species to find food, whereas subordinates avoid resources that dominants frequent in order to avoid physical attack [28,29].

know of being that of the alpheid shrimp that relies on its goby partner to detect danger, and perishes without it [51,71].

Conclusions

Information flow between species can influence the position in space and time of different species, whether it be temporary groups around a predator or resource or stable associations between species in mixed-species groups or between species with shared territorial locations. Although animals can associate in groups of species that share information equally, information transfer in groups is often asymmetrical, flowing from information sources to information seekers. The differences among species in the information available to other species are driven by major interspecific morphological, ecological and behavioral differences, which determine the value of information and the manner in which animals gather, produce and transmit that information.

There is currently too little information, much of it qualitative, on the relationship between information and community structure. Suggestions as to why some species

play important roles in mixed-species associations are often qualitative and untested, and there is a danger in accepting 'just-so' stories simply because they are plausible. We need data that specifically compare species in the information they can provide to other species. A start has been made in this direction in comparing the alarm calls of birds and heterospecific responses to them [16,72–74].

A second step in future research is to better quantify the associations among species and their dependence on each other. Whereas information on the dependence of species in mutualisms is often well studied, the interdependencies of species in mixed-species groups are less well understood. Species can either be experimentally removed from systems [75] or their presence simulated [6] to better understand their effects on others. Alternatively, the co-occurrence of species can be compared to null models [12,76], or mixed-species associations examined through social network theory [77]. A final step for research then would be to determine whether information production actually predicts species associations, specifically investigating the issues outlined above in 'testable hypotheses.'

The question of information and community structure is not purely an academic one. As conservation strategies progress from species-by-species plans to community-wide management [78], it is essential to understand the interdependencies of species, and whether certain species play keystone roles [79]. Since the evidence is strong that interspecific information transfer influences the distributions of animals relative to each other, as evidenced by the number of studies referenced herein, knowledge of interspecific information might aid to conserve current global biodiversity and plan how to respond to environmental change.

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