Interspecific Communication

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Introduction

Interspecific communication usually deals with signals that provide a receiver with information about the heterospecific sender, which includes the sender's aggressive intentions in the case of interspecific aggression, territorial status, which can be important in the case of interspecific competition (undoubtedly a common interaction among animals), suitability as a mate in the case of interspecific hybridization, and current actions which are important signals for the coordinated activities of group members to maintain group cohesion. Interspecific communication may also deal with signals in which the sender provides the heterospecific receiver with referential information about objects external to itself. Such objects could be other individuals of the same trophic level, accessible resources such as food, or predators.

Most often interspecific signaling occurs between ecologically related species which usually belong to the same guild, to alert both conspecifics and heterospecific members of mixed-species groups of potential danger and recruit nearby individuals for mobbing defense. Examples include mixed troops of monkeys, mixed-species flocks of birds, and fish schools in the tropics. However, interspecific communication can also occur between nonadjacent trophic levels to warn a predator that it has been spotted, or involve prey individuals signaling to the predators of their predators. In some cases, signal use occurs between species of the same or similar trophic levels, but under circumstances that do not involve individuals of the same social group. This is called eavesdropping, also known as information parasitism, which occurs when an individual other than the intended receiver cues in on public sensory information.

Within-Trophic-Level Interspecific Communication

Within-Trophic-Level Social Integration Signals of Heterospecific Animals

There is a variety of social contexts in which individuals belonging to two or more species must integrate their activities to achieve a common goal. Protection against predators is among the most important reasons for individuals to become members of a multispecies group. The integration of members of group-living heterospecifics to maintain group cohesion, to coordinate movement, and to organize communal activities of all members of multispecies groups should be synchronized in such a way that they enhance predator protection. Social integration requires recognition of key target individuals (such as conspecific and heterospecific group members), appreciation of both interspecific and intraspecific dominance hierarchies, and honest signals. For example, mixed-species aggregations of breeding birds and mixed-species foraging groups may result from an active search for heterospecific companions. Recognition of neighboring species is involved in these assemblages. It is well established that birds actively aggregate in mixed-species foraging groups to gain protection against predators and/or enhance feeding efficiency, supporting the view that positive ecological interactions are important in structuring some breeding bird communities.

Signaling an internal state to heterospecifics

Many animals stay as members of mixed-species groups where interspecific competition restricts access both to food and to the safest and most preferred feeding sites. In such groups, the position of the individual in the group's intraspecific and interspecific dominance hierarchy affects its resource access and survival. Larger animals are usually more dominant in interspecific dominance hierarchies. Given the stability of interspecific dominance hierarchies, the individual's ability to recognize aggressive intentions by heterospecific group members allows a potential threat posed by more dominant individuals of other species to be more easily recognized. The ability to understand the aggressive signaling by other species makes the groups consisting of heterospecific individuals more coherent and decreases the probability of overall aggressiveness and being injured during the interference competition between social species.

Interspecific signaling of mating and territorial status

Animals living in complex communities need to be able to identify other species and retain memories of species identities for long periods of time to make optimal choices. The ability to discriminate between conspecifics and heterospecifics may be crucially important in the refinement of mating preferences during speciation and for premating isolation of sympatric species. Various species defend territories not only against conspecifics but also against certain other, usually congeneric, species. In birds, interspecific interactions over territoriality are effected through interspecific reactions to territorial songs. Where *Regulus* species are interspecifically territorial in Spain, both goldcrest (Figure 1), *Regulus regulus*, and firecrest, *R. ignicapillus*, can sing species-specific or mixed songs, and most males react aggressively to the song of the other species. This example shows how song convergence between two species of songbirds may play an important role in resource partitioning by signaling to a heterospecific competitor. Recently, it has been shown that male blackcaps (Figure 2) *Sylvia atricapilla*, can associate species-specific songs with species-specific plumage and that they can retain the memory of this association for an 8-month period without contact with heterospecific rivals, indicating that signals from two different sensory modalities (visual and auditory) are important for distinguishing conspecifics from heterospecifics.

Multispecies group integration

Group living serves a variety of adaptive functions and social animals need special signals to coordinate their movements and other activities to facilitate social benefits such as warning and defense against predators. The level of group integration depends largely on mechanisms used to recognize group members and signals used to maintain group cohesion. When group membership is unstable, a group label is meaningless and groups are more appropriately called aggregations. Examples include swarms of insects, migratory flocks of birds, and herds of antelopes.

In contrast, group labels can be critical in socially cohesive mixed-species assemblages. Individual recognition based on familiarity with group members is a common mechanism used to distinguish group members from nonmembers. Groups must be relatively small and stable in composition for this mechanism to operate. In multispecies groups, individual recognition facilitates the development of stable dominance hierarchies within groups because each individual can remember the outcome of prior encounters with other members. In mixed groups of the tits (*Paridae*), crested tits (Figure 3), *Lophophanes cristatus*, usually dominates over willow tit (Figure 4), *Poecile montanus*, individuals. In some cases, willow tits may rise in rank above crested tits by demonstrating aggressive postures and giving aggressive calls, and these changes in dominance hierarchy are permanently accepted by all crested tits.

Figure 1 Goldcrest, *Regulus regulus.*

Figure 3 Crested tit, *Lophophanes cristatus.*

Figure 2 Blackcap, *Sylvia atricapilla.*

Figure 4 Willow tit, *Poecile montanus.*

Coordination of multispecies group movement

For the majority of group-living species, the advantages of grouping can accrue only when group members remain in close proximity. When groups move over large areas as a unit, mechanisms for maintaining group cohesion are required. The signals used to coordinate group movement vary depending on the function of grouping, the precision required, and the mode of locomotion. In a wide variety of social species, three types of vocalizations are found: (1) soft, frequently repeated contact calls with individual signature, (2) louder and longer separation calls by individuals that have become separated from the group, and (3) movement initiation calls, which are the loudest of the three types and are structured to be easily localizable. The existence of such vocalizations is consistent with the ideas of Marler about signal design features and motivation–structure rules proposed by Morton suggesting that selection would favor the use of tonal, high-frequency vocalizations in fearful and friendly contexts because these sounds symbolize smaller size or juvenile age class, thus reducing the likelihood of attack by the receiver of the call.

Within-Trophic-Level Interspecific Referential Communication About External Objects

Mixed-species groups are often observed in birds, primates, and cetaceans. However, direct measurements of the fitness value of gregariousness and the understanding of principles of interspecific communication in these animal species are still in their infancy. Predation represents a strong selective factor in prey populations, resulting in the development of complicated and unique behavioral defenses. The trade-off between maintaining antipredator vigilance and devoting resources to other activities has been ameliorated in many group-living species by the development of calls accessible to members of a local community. The most important signals about external objects used in heterospecific company include resource-recruitment signals, distress signals, and alarm signals. Alarm signals can be further categorized as low-risk warning signals, which may be followed by on-guard signals, inspection or mobbing signals, and high-risk warning signals.

Resource-recruitment signals

A variety of social primates and birds produce a food call while at the location of a newly found food source. Call rates usually increase with food preferences and quantity found. In primates, an individual out of sight of other group members is more likely to produce a discovery call than one with others nearby. This suggests that the calls are used to ensure sufficient group sizes for predator surveillance during feeding. However, actual field data on food calls among individuals belonging to different species are surprisingly rare, despite the fact that social foraging should reduce the risk of energetic shortfall, and that resource-recruitment signals are well known among members of groups consisting of a single species. Nonetheless, such calls might be expected to evolve because some associations composed of heterospecific animals (such as mixed-species flocks of temperate tits and mixed-species associations of dolphins) are most convincingly explained by the foraging advantage hypothesis.

Alarm calls

Alarm calls are among those signals that are usually shared by ecologically related sympatric species. Mixed-species associations can reduce group members' risk of predation through dilution effects, predator deterrence, and improved detection. However, a positive association between the group size and predator detection efficiency relies on the ability of the members to communicate. For this reason, the evolution of social complexity is often associated with the evolution of a large vocal alarm repertoire. Not surprisingly, such animals as passerine birds, primates, and cetaceans having large alarm call repertoires are predisposed to grouping with heterospecifics and responding to heterospecific alarm calls. Defining sociality as group living in which members interact and form relationships, several researchers have found that recognition of heterospecific alarm vocalizations is an essential component of antipredator behavior, especially in primates. Their alarm calls are very similar structurally, and all members of a mixed troop respond to any species' alarms.

Several studies have shown that the forest wintering tits save vigilance time not only by flocking with conspecifics but also by associating with other tit species, goldcrests and treecreepers, *Certhia familiaris*. Heterospecifics in such mixed-species flocks are generally considered to substitute for conspecifics as predator protection at lower competition cost. However, this poses several important questions related to the causes of alarm calling when in the company of heterospecific individuals. Will members of multispecies groups give alarm calls irrespective of the absence of conspecifics? Will an individual belonging to one species warn individuals belonging to the other species – in other words, how reliable are heterospecific alarm calling? It is possible that even within the same flock, the compensatory benefits of emitting warning signals may vary with the participant, which suggests that the field of alarm calling among heterospecifics and the origin and evolution of warning communication are still puzzling and largely unanswered.

Mobbing behavior

A simple definition of mobbing is the development of an assemblage of individuals around a potentially dangerous predator. In 1960s, the eminent Austrian ethologist Konrad Lorenz used the English term mobbing to describe the behavior that animals use to scare away a stronger, predatory enemy: 'a number of weaker individuals crowd together and display attacking behavior, such as geese scaring away a fox.' This well-defined behavioral pattern occurs in a wide diversity of animals, especially in birds and mammals. If two territorial neighbors cooperate during mobbing, they have an increased opportunity to drive the predator from their breeding area. Under natural conditions, mobbing often occurs in a company of heterospecifics and they benefit from the antipredator behavior of other species. This implies that individuals belonging to different species should recognize mobbing calls of other species and that there is a possibility of reciprocity among heterospecifics. This is so because the emission of mobbing signals puts the mobber in jeopardy, and an altruistic act helping a nonrelative only pays the altruist if it is directed at a particular heterospecific individual that on a later occasion reciprocates. Although human behavior abounds with reciprocal altruism, few examples exist documenting reciprocal altruism in animals, while experimental evidence on interspecific mobbing as a reciprocity-based behavior is so far lacking.

Within-trophic-level distress signals

Prey individuals often give distress calls in the final stages of predator attack or being caught in a trap. These signals are fundamentally different from alarm calls and mobbing calls. Among avian species, distress calls are notably similar in structure, generally consisting of short, screaming repeated bursts of unmusical sound covering a wide range of frequencies, characteristics that increase the effective distance and localization of the call. The calls seem to be convergent among different bird species. Parents of many animal species will respond to distress calls of their own offspring. However, intraspecific responses by the vespertilionid bats, *Pipistrellus pygmaeus*, showed that they respond to the distress calls of unrelated conspecifics, thus rejecting the hypothesis that distress calls request aid from kin. Moreover, some authors have observed interspecific responses to the distress calls of the phyllostomid bat, *Artibeus jamaicensis*.

A number of hypotheses have been put forward to explain the function of distress calls. Some of the explanations require strong reciprocity links between sender and receiver before it pays a receiver to respond. For example, an individual giving distress calls may warn other heterospecific individuals of the presence of a predator, provide other individuals with information about a predator (and thus reduce the chance of those individuals falling prey to a predator in the future), or attract other individuals that will mob a predator (which may in turn facilitate the caller's escape). Distress signals may therefore resemble a request of aid from reciprocal altruists. While there is some evidence for these hypotheses, within-trophic-level distress calling has not, to date, been studied in detail.

Within-trophic-level interspecific eavesdropping

Animal communication networks can be extremely complex, consisting of many signalers and many receivers. The idea about communication network follows from the observation that many signals travel further than the average spacing between animals. This is self evidently true for long-range signals, but at a high density the same is true for short-range signals such as begging calls of nestling birds. Growing evidence clearly shows that alarm calls elicit responses not only from conspecifics but also from eavesdropping heterospecifics. If an individual intercepts information from the alarm calls directed toward another individual, this is termed 'interceptive eavesdropping.' This differs from 'social eavesdropping,' which involves obtaining information from an interaction between two signalers. Numerous studies have shown that mammals, birds, amphibians, and fish recognize alarm signals of other species, and interceptive eavesdropping can even occur between taxa that are not closely related. For example, vervet monkeys, *Cercopithecus aethiops*, respond to the alarm calls of superb starlings, *Spreo superbus*; dwarf mongooses, *Helogale parvula*, recognize hornbill, *Tockus* spp., alarm calls; and red squirrels, *Sciurus vulgaris*, respond to the alarm calls of jays (**Figure 5**), *Garrulus glandarius*. Although these examples show the ability of many animals to recognize the alarm calls produced by other species, the amount of information they glean from these eavesdropped signals is largely unknown.

Instead of using a general type of alarm call, some species have categorically distinct vocalizations that are each associated with a different type of predator encounter (e.g., different calls that refer to aerial vs. terrestrial predators). There are a few studies that show that birds and mammals discriminate among categorically distinct types of heterospecific vocalizations. For example, the closely related Diana monkeys, *C. diana*, and Campbell's monkeys, *C. campbelli*, recognize each other's acoustically distinct leopard and eagle alarm calls and treat them

Figure 5 Northern (or Eurasian) jay, *Garrulus glandarius.*

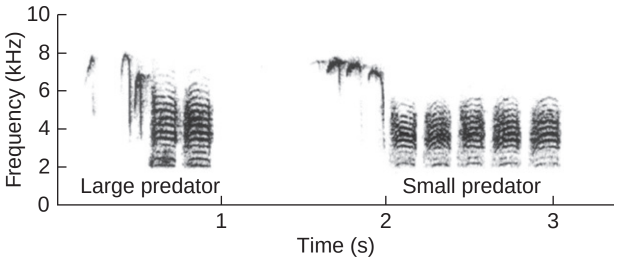

Figure 6 Chickadee (*Poecile atricapillus*) alarm calls encode information about predator size and risk.

similar to conspecific alarm calls. A sympatric bird, the yellow-casqued hornbill, *Ceratogymna elata*, also differentiates between these two types of monkey alarm calls. Similarly, vervet monkeys discriminate among the aerial and terrestrial predator alarm calls of superb starlings.

Instead of or in addition to using acoustically distinct vocalizations, some animals encode considerable information about predators in more subtle variations of a single type of call. It was recently shown that *chick-a-dee* alarm calls (Figure 6) of black-capped chickadees, *P. atricapillus*, encode a surprising amount of information about the size and threat of a given predator through variations in the acoustic structure of the calls, demonstrating that chickadees have one of the most sophisticated mobbing call systems yet discovered.

Complex information, including predator size and type, can potentially be gleaned from these calls by heterospecific individuals. This idea is supported by experimental work revealing that red-breasted nuthatches, *Sitta canadensis*, a temporary flock-mate of black-capped chickadees, respond appropriately to subtle variations of these '*chick-a-dee*' calls, thereby showing that they have gained important information about potential predators in their environment. These findings clearly demonstrate that our knowledge about complexity and adaptiveness of communication between species is surprisingly superficial.

Intertrophic-Level Interspecific Communication

Signals exchanged by animals within the same trophic level are likely to be cooperative in the sense that the sender is providing useful information to the receiver, whereas signals exchanged between trophic levels occur when conflicts of interest between sender and receiver may be really high. This guarantees signal honesty, which is required before the receivers attend to the signal. Many animals give signals often to individuals belonging to species of different trophic levels (prey individuals vs. predators). Such signals can be divided into those that cause a receiver to approach the sender and those that encourage the receiver to repel.

Interspecific Attraction Signals

Distress signals

A number of animals give loud distress calls when attacked by predators. Some may release pheromones from damaged tissues as soon as they are attacked. Growing evidence suggests that most animal distress signals function to attract predators other than the one attacking the distressed individual. If the additional predators distract or interfere with the first, the prey may have a chance to escape. A more complex function of distress signals is the attraction of predators of the attacking predators. This could be viewed as behavioral manipulation, although there are no definitive examples of this manipulation. However, such interactions have been described in a system consisting of plant, herbivore and herbivore's parasites or predators.

Interspecific Repellent Signals

Notification of predator detection

A signal emitted in the presence of a predator could be not only an alarm intended to warn other prey individuals, but it can also be designed to deter the predator from attack. Stalking predators rely on surprise, and if a prey individual detects a predator and signals this fact to it, the predator usually gives up its current hunt, since it is now likely to be unsuccessful. Loud alarms of a variety of birds and primates, foot stamping by kangaroo rats, and tail wagging by many lizards, all appear to be signals to notify a predator that it has been detected. Ground squirrels have recently been shown to signal to potential predatory rattlesnakes by waving their tails that they have heated through increased blood flow. Clearly, a predator will attend to such signals only if they are largely honest. Prey individuals that perform the signal repeatedly, whether a predator is stalking or not, risk having their signal ignored by the predator. Therefore, many prey animals give just a few calls, which are usually enough to signal to the predator that it has been spotted.

Predator inspection and mobbing

In many animals, calls of notification of detection may be followed by predator inspection. Predator inspection ensues when the assembled prey conspicuously monitor the predator's subsequent activities, which is often followed by mobbing in some species. Mobbing alarm calls are produced in response to perched raptors or terrestrial predators. Mobbing behavior may have several different functions, but one of the most important is that the mobbing is likely to harass the predator enough to drive it from the area so that it does not surprise the birds later. This view is supported by anecdotal observations suggesting that when mobbing perched raptors, passerine birds tend to approach more dangerous stationary predators more closely than less dangerous ones, probably in order to ensure its desertion from the vicinity.

Notification of condition

Prey in good enough condition to escape pursuit may benefit by signaling this fact to a predator when it has already begun an attack. Prey that failed to signal would therefore be at a disadvantage, thus providing a strong incentive for prey in poor condition to cheat and produce the signal regardless of condition. Predators, in turn, should rely on such signals only if they are honest indicators of condition. One mechanism that would ensure signal honesty is the 'handicap principle': honesty is ensured if the signal is sufficiently difficult or costly to produce that only high-quality prey are able to produce it. This appears to be the case for the jumping gait called stotting used by a number of African antelopes. Once wild dogs begin a chase, some Thompson's gazelles, *Gazella thomsoni*, stot and some do not, and those that do, stot at different rates. The stotting itself neither hinders nor helps the gazelle to escape once it is chased by a dog. However, it appears to be difficult for a gazelle in poor condition to stot at high rates. Wild dogs preferentially focus their chases on gazelles with lower stotting rates. In contrast, Thompson's gazelles rarely stot for stalking cheetah, in which the attack is quick and there is little time for targeted prey to respond before the predator is upon them.

Aposematic signals

Animals armed with unpalatable and even toxic spines often exhibit conspicuous colors or behavioral patterns. Such aposematic signals are clearly aimed at discouraging predators from attacking the senders of such signals; these senders are usually highly conspicuous against the relevant background. Many salamanders, butterflies and other insects, frogs, and skunks are well-known examples.

Eavesdropping of prey signaling by predators

Interspecific eavesdropping by predators and parasites is common and occurs in all sensory modalities. Many mating systems are characterized by conspicuous male sexual displays, where males aggregate and advertise acoustically to attract mates. Chorusing as an example of male aggregation and sexual display is especially prevalent in anurans. Males in aggregations might have advantages in attracting females over males advertising alone. There are also disadvantages to males that join choruses. Several studies have shown that acoustically advertising anuran males have a higher probability of attracting predators such as frog-eating bats, *Trachops cirrhosus*, and philander opossums, *Philander opossum*. Recently, it was confirmed that white storks, *Ciconia ciconia*, could discriminate the signals of moor frogs, *Rana arvalis*. This suggests that such predators as frog-eating bats, storks, opossums, and even blood-sucking flies (Figure 7), *Carothrella*, are acoustically orienting predators during the reproductive season of frogs and that chorusing is costly in terms of predation.

Figure 7 (a) *Carothella* blood-sucking flies attacking tungura frogs. (b) Closeup of a fly on a frog's nose.

Learning of Heterospecific Signals

Alarm signals contain some of the most pertinent information an animal can learn about its environment: the presence of a predator. Thus, an animal that is able to eavesdrop on the alarm signals of another species may obtain considerable, potentially even life-saving, information. This response could be innate and may be triggered by acoustical properties shared between alarm calls. Playback experiments with apostlebirds, *Struthidea cinera*, suggested that experience with a particular species' call is not essential to elicit mobbing; rather, intrinsic aspects of the calls themselves may explain heterospecific recognition.

The heterospecific response can result also from a learned association between predator presence and alarm calls. This was supported while examining the role of learning in the discrimination of heterospecific vocalizations by wild bonnet macaques, *Macaca radiata*, in southern India. The bonnet macaques' flight and scanning responses to playbacks of their own alarm vocalizations were compared with their responses to playbacks of vocalizations of Nilgiri langurs, *Trachypithecus johnii*; Hanuman langurs, *Semnopithecus entellus*; and sambar deer, *Cervus unicolor*. Age and experience appeared to be important factors in heterospecific call recognition by bonnet macaques.

Some other studies of heterospecific eavesdroppers such as the Galapagos marine iguana, *Amblyrhynchus cristatus* (that does not emit any kind of vocalization or auditory alarm signal); the golden-mantled ground squirrel, *Spermophilus lateralis*; the red squirrel, *S. vulgaris*; and Gunther's dik-dik, *Madoqua guentheri* (which do not live socially) also support the idea that the learning of heterospecific alarm signals is important and suggest that sociality is not always a necessary prerequisite for the evolution of flexible associative learning abilities.

See also: Agonistic Signals; Alarm Calls in Birds and Mammals; Communication Networks; Dolphin Signature Whistles; Dominance Relationships, Dominance Hierarchies and Rankings; Ethology in Europe; Food Signals; Group Foraging; Group Movement; Honest Signaling; Konrad Lorenz; Referential Signaling; Rhesus Macaques; Social Learning: Theory; Túngara Frog: A Model for Sexual Selection and Communication; Vocal Learning.

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