

## Chapter 7

# Leadership and Sentinel Behavior

### 7.1 INTRODUCTION

In any social organization, the question comes naturally as to whether different members of the group play different roles. Army units and management teams, to take two well-known cases in human groups, are clearly composed of individuals playing strictly defined roles. In fact, the effectiveness of the unit or team often is critically dependent on clearly defined role boundaries for each group member. The unit or team typically has a task to perform, and roles are assigned by a third party to achieve this goal. Lacking immediate goals and with no external role assignment, can we expect to see similar roles in mixed-species groups (MSGs)?

To assess this issue, it is important to make a distinction between fixed and flexible roles. We refer to fixed roles in an MSG as those that follow from particular attributes of a species, attributes that are apparent regardless of whether the species is inside or outside of an MSG, or, if inside such a group, what is the composition of that group. The occurrence of fixed roles reflects the simple fact that different species in an MSG are not clones of one another and can show substantial variation when it comes to searching for resources or allocating time to vigilance. Reflecting this variation, some species are more attractive to other species when it comes to forming an MSG. One example of a fixed role in an MSG is food flushing. A particularly dynamic species in such groups can disturb prey during its foraging making them available to nearby species (Belt, 1874; Struhsaker, 1981; Sazima et al., 2007; [Sections 3.6.1 and 4.2.2](#)). The role of food flusher was not devised to increase the effectiveness of the group in generating resources but reflects rather the natural foraging behavior of some species, which remains in the same shape and form regardless of whether other species are present. Similarly, some species in MSGs act as sentinels for predator detection (Munn, 1986; Ragusa-Netto, 2002). The sentinel role is not assigned by decree to optimize predator detection at the group level. Instead, this role might reflect the natural tendency of a species to forage in the higher stratum of the habitat or to use a foraging technique that allows individuals to concurrently monitor the surroundings (Martínez and Zenil, 2013).

A flexible role, by contrast, is one that occurs specifically in the MSG context and that provides benefits to the species playing that role and, sometimes, incidentally, to other species in the group. This would be the case if a species, say, only acted as a sentinel in the presence of other species or switched foraging mode in an MSG to flush prey. Obviously, such roles have not evolved or are not performed to ensure the better functioning of the MSG, as would be the case for a unit or a team with a specific task to perform. When thinking about flexible roles, it is conceivable that some species evolved traits or can modify existing traits to make them more suitable to play certain roles in such groups. Traits associated with flexible roles should allow individuals that possess them to increase their own success when participating in an MSG.

In this chapter, we examine the occurrence of roles in MSGs and whether there is any evidence that roles are flexible rather than fixed. Two roles in particular have attracted much attention in the context of MSGs: leadership and sentinel behavior. Leadership is believed to facilitate the formation and cohesion of MSGs. Sentinel species act as an early warning system to detect predators. Much of the evidence for roles in MSGs comes from the avian literature, but the concept of roles also applies to other types of species such as fish (Strand, 1988; Sazima et al., 2007) and primates (Cords, 1990; Bshary and Noë, 1997; Smith et al., 2003).

## 7.2 LEADERSHIP

### 7.2.1 Historical Perspective

Early naturalists clearly noted that different species in MSGs play different roles. For instance, in his book detailing his trip to the Amazonian jungle, Henry Walter Bates recalled how the indigenous people thought that a little gray bird fascinated the rest of the group and led them across the jungle (Bates, 1863). Not surprisingly, no such species could ever be located, but clearly the question as to whether one species in an MSG plays a leadership role attracted attention early in the literature.

Avian MSGs that form in the more open habitats of Australia also appeared to coalesce around a few species of thornbills, which were labeled “association formers,” whereas other species were characterized as “joiners” (Gannon, 1934) (Table 7.1). Gannon also suggested that calls from thornbills attracted other nearby species. Also in Australia, Hindwood (1937) noted that one species tended to initiate most movements in MSGs. In deciduous forests of Europe, the incessant movement of tit species was believed to attract other nearby species (Delamain, 1933).

In view of such differences among species in the ability to lead groups, Winterbottom (1943) distinguished between nucleus and circumference species to describe species that formed the core of MSGs in African woodlands and those that only joined groups occasionally and tended to occur at the periphery, respectively. The nucleus species typically foraged in monospecific groups

**TABLE 7.1** A Lexicon of Terms Used to Describe Leadership Roles in MSGs

Terms	Definition	References
Association former	A species that facilitates the formation of MSGs	Gannon (1934)
Association joiner	A species that tends to join other species in MSGs	Gannon (1934)
Nucleus species	A species found at the core of MSGs	Winterbottom (1943)
Circumference species	A species found at the periphery of MSGs and typically less frequent than the nucleus species	Winterbottom (1943)
Accidental species	A species more rarely encountered in MSGs	Davis (1946)
Nuclear species	A species that facilitates the formation and cohesion of an MSG	Moynihan (1962)
Regular attendant species	A species that occurs regularly in an MSG but shows no leadership quality	Moynihan (1962)
Long-term follower	A species that follows an MSG over an extended period of time (similar to regular attendant species)	Buskirk et al. (1972)
Occasional attendant species	A species that occurs occasionally in an MSG but shows no leadership quality	Moynihan (1962)
Short-term follower	A species that follows an MSG for a short period of time and over short distances (similar to occasional attendant species)	Buskirk et al. (1972)
Active species	A species that more often joins other species than it is joined by others	Moynihan (1962)
Passive species	A species that is more often joined by other species than it joins	Moynihan (1962)
True leader species	A species that is followed by others much more than it joins others	Morse (1970)
True follower species	A species that follows others much more than it is joined	Morse (1970)
Sentinel species	A species that maintains high vigilance against predators from a vantage point	Westcott (1969), Conner et al. (1975), Munn (1986)

MSGs, mixed-species groups.

and also occurred frequently outside MSGs. Circumference species were also labeled as accidental in descriptions of avian MSGs in Brazil a few years later (Davis, 1946). Davis also identified one particularly vocal species commonly found in most groups and who seemed to act as a leader. These early descriptions clearly suggest that different species occur to different extent in MSGs and that some traits, such as calls or energetic movements, probably facilitate the formation and cohesion of these groups.

The classification of roles in MSGs took a more prominent turn after the publication of a review on the evolution of MSGs in Neotropical birds (Moynihan, 1962). In his classification scheme, Moynihan recognized nuclear and attendant species (Table 7.1). Nuclear species form the core of the groups, and these species are believed to be important for the formation and cohesion of these groups. Attendant species can be found regularly or more occasionally in these groups and play a more minor role in leadership. Moynihan also distinguished between active and passive species. An active species tends to join more often than it is joined by others, whereas a passive species tends to be joined more often than it itself joins. The passive, nuclear species would thus be the most important species in the formation of MSGs and might possess or evolved traits that facilitate grouping. Moynihan further speculated that such leaders possessed specific traits such as many contact calls, nonaggressive interactions, and dull plumage. Influential reviews on MSGs still refer to the scheme proposed by Moynihan minus the distinction between active and passive species (Diamond, 1981; Powell, 1985; Terborgh, 1990; Hutto, 1994; Greenberg, 2000). How to practically distinguish between different types of attendant species and how regularly they attend MSGs relative to their abundance outside such groups also represent an active field of research (Farley et al., 2008).

### 7.2.2 How to Quantify Leadership

The obvious question about leadership is how to distinguish between leader and follower species. Moynihan provided a list of qualitative traits for classifying species into different roles. However, without a quantitative way of classifying species as leaders or followers, it is difficult to move beyond subjective impressions. Various ways have been used over the years to assess leadership in MSGs in a more quantitative fashion, and these are reviewed below.

We restrict our discussion to MSGs involving more than two species. The reason for this is simple: in groups with two species, leadership is often totally confounded with foraging mode. A food-flushing species leads by default because the other species must follow it to obtain the flushed prey. As an example, due to their large size and their relative wasteful feeding habits, many primate species flush or drop food for other species, including birds and mammals (Heymann and Hsia, 2015). In nearly all such cases, the nonprimate species follows the primate species. Relationships of this kind are also common in coral reefs in which a variety of fish that disturb the surface of the

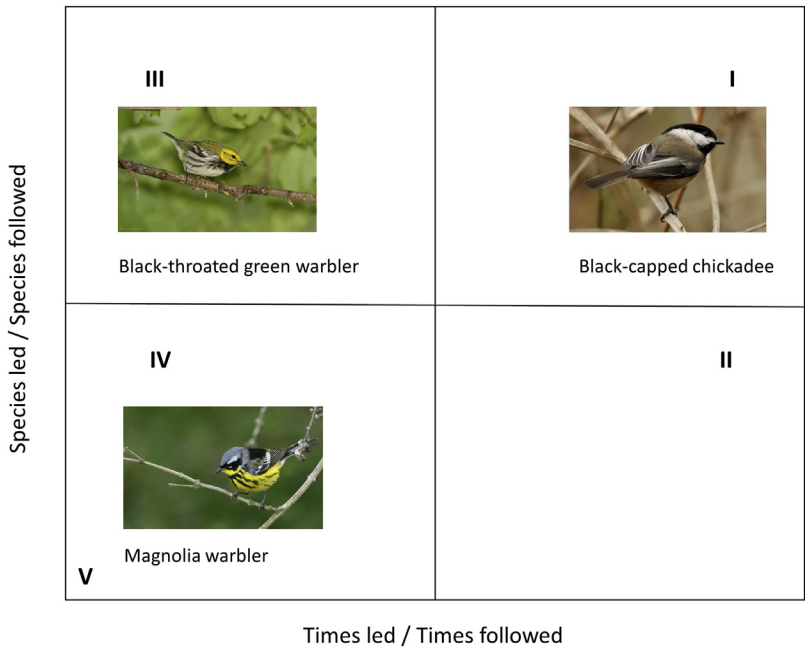
reef, releasing food particles, are followed by other species (Sazima et al., 2007). Although obligate following of this kind can also occur to some extent in groups involving more than two species, it is probably less likely because foraging modes are more diverse and the benefits of joining a group with more species are not just limited to flushed prey. Another potential confounding factor in two-species groups is dominance. The species that leads might be the one that has access to resources first due to higher dominance, as seems to be the case in some primate MSGs (Heymann and Buchanan-Smith, 2000). Again, strict dominance is less likely to affect leadership in groups with more species. For similar reasons, we also exclude mixed-species associations that aggregate around resources. In this sort of groups, some species uncover resources that then become available to other nearby species (Chapter 2). Both dominance and foraging mode typically determine which species uncover resources and those that subsequently follow.

### 7.2.2.1 Quantitative Assessment

The classification scheme proposed by Moynihan is purely qualitative and cannot really be used practically to identify roles in MSGs. When using this scheme, most researchers simply look for traits that are presumed to be important for the formation and cohesion of groups (Section 7.2.3). A species should also occur frequently in MSGs to at least qualify as nuclear. The classification of a species as a leader or as a follower too often remains a qualitative exercise fraught with ambiguity (Willis, 1972).

Morse (1970) on avian MSGs in temperate forests of North America developed a more quantitative approach, which addressed some of these shortcomings. Morse proposed two indices for each species in an MSG: (1) the ratio of the number of species led to the number of species followed and (2) the ratio of the number of times individuals of the species led to the number of times they followed (Fig. 7.1). Depending on the values of these ratios, Morse distinguished between true leader and true follower species, and those in between. A true leader species often leads and is frequently followed by several species, whereas the reverse is true for a true follower. True leaders would be characterized as passive nuclear in Moynihan's scheme, whereas true follower species would represent the active attendant species in that scheme.

Morse's approach is limited to cases where it is possible to unambiguously determine when one individual leads and another follows. Morse determined a leader and a follower in interactions between individuals of two particular species based on the latency to respond to a movement initiated by one individual. Morse did not specify how closely in time a joining event should follow the initial movement. What is also missing is a sense of the direction taken by the follower species after the initial movement by the leader species. Presumably the movement must be made in a similar direction, but again it was not clear how far would a follower have to stray before the movement was discounted as a following event.



**FIGURE 7.1 Leadership in mixed-species groups (MSGs).** Classification scheme proposed by Morse (1970) to assess leadership in MSGs. Species are characterized by two ratios: the ratio of the number of species led to the number of species followed, and the ratio of the number of times individuals of a species led to the number of times they followed. True leader species can be found in the upper right quadrant (I), whereas true follower species can be found in the lower left corner (V). In Maine woods, the black-capped chickadee led most MSGs; the black-throated green warbler, in quadrant III, led fewer times but attracted more species than the magnolia warbler in quadrant IV. No species fitted in quadrant II. *Photo credits: Black-capped chickadee (Brendan Lally), black-throated green warbler (Bill Majoros), and magnolia warbler (Isaac Sanchez).*

Perhaps the greatest difficulty with the ratio approach proposed by Morse is that it fails to take into account the frequency with which different species interact in MSGs. Two different species might have the same ratio of the number of times the species led to the number of times it followed even though one species could lead and join many more times than the other. In short, the use of ratios cannot distinguish between a species that is followed by many species when it leads but who leads infrequently and those that are equally attractive to other species but lead more frequently. Similarly, ratios are independent of the amount of time spent in an MSG. A case for a leader species would be stronger if for the same ratio the leader and follower species interacted over several hours as opposed to minutes. Time spent interacting was indeed proposed as a way to classify interactions in fish MSGs (Pereira et al., 2012), implying a need to consider how long species remain together while foraging. The ratio approach proposed by Morse has rarely

been adopted by other researchers. Nevertheless, the general idea of using data on which species follow others is simple and useful to get a first sense of leadership in an MSG.

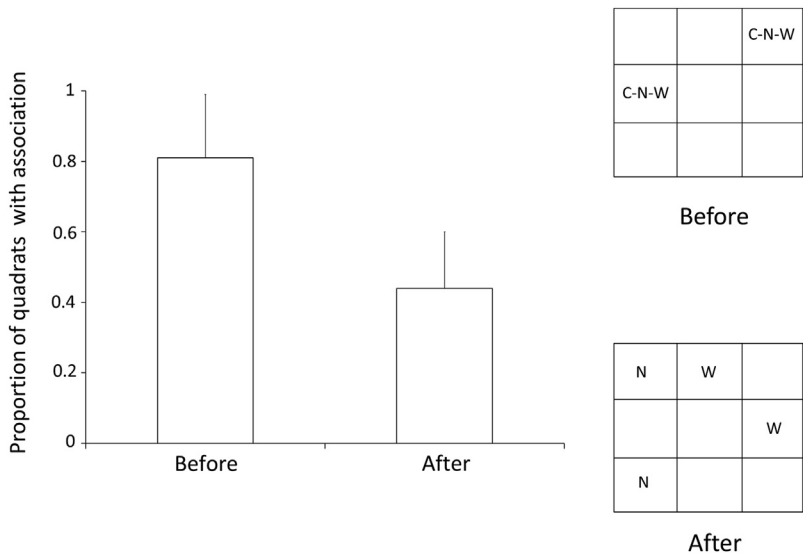
Another approach to quantifying leadership consists in correlating the movement of a group across the habitat to the movement of an alleged leader species. The movement direction adopted by the group is expected to match the movement direction taken by the leader species rather than by follower species. Close matching of this kind was observed in MSGs including the tufted titmouse, a presumed leader species (Contreras and Sieving, 2011). This approach is best suited to less obstructed habitats in which the direction of movement can easily be determined over long distances.

### *7.2.2.2 Experimental Manipulation*

If a species plays an important role in the formation and cohesion of MSGs, MSGs without a leader species should be less likely to form or persist. Observational evidence suggested that in areas where leader species are absent, MSGs are less frequent and show a different organization (Stouffer and Bierregaard, 1995; Maldonado-Coelho and Marini, 2004; Zhang et al., 2013). Because absence of the leader species might reflect factors that also affect follower species, experimental evidence is needed to isolate the effect of leader species on MSGs. An experimental approach holds much promise to avoid the pitfalls associated with observational studies of leadership.

In one of the few experiments carried out to investigate whether leader species really are involved in the formation and cohesion of MSGs, researchers removed putative leader species from woodlots in eastern North America and documented subsequent adjustments by the remaining species. Earlier observations suggested that the tufted titmouse and the Carolina chickadee lead these MSGs. Various species of woodpeckers and nuthatches typically coalesce near these species during foraging. In woodlots where leader species were removed (and relocated elsewhere), close spatial associations between various follower species occurred less frequently than in woodlots where the leader species remained (Fig. 7.2), showing the importance of leader species for the formation of MSGs in these woodlots (Dolby and Grubb, 1999). This finding should not be interpreted as evidence that leader species actively recruited other species to form groups in these woodlots. Passive attraction would be sufficient to form MSGs in this case. We will return to this study once more in discussing the conservation implications of MSGs (Section 8.4).

Experiments have also focused on putative signals made by leader species that facilitate the formation of MSGs. Such signals can be visual or vocal (Section 7.2.3). If visual signals are important to attract other species, masking such signals should affect the formation of MSGs. If vocal signals play an important role, playback of such signals should attract other species. Several studies used an experimental approach to examine these predictions.

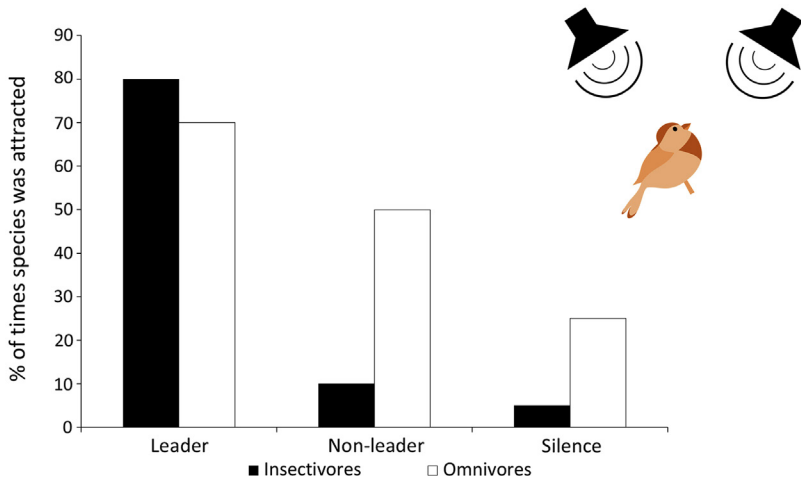


**FIGURE 7.2 Formation of mixed-species groups.** The proportion of quadrats in a woodlot in which follower species occurred together decreased after the leader species were relocated elsewhere. In the schematic representation of the experiment on the right panel, the letter C refers to chickadees, the leader species, and the letters W (woodpeckers) and N (nuthatches) refer to follower species. Means and standard error bars are shown. *Adapted from Dolby, A.S., Grubb, T.C., 1999. Functional roles in mixed-species foraging flocks: a field manipulation. Auk 116, 557–559.*

The white-flanked antwren is a gregarious bird commonly found in the tropical forests of Central and South America. This species has long been thought to act as a leader of large understory MSGs (Moynihan, 1962; Wiley, 1971; Willis, 1972; Jones, 1977; Munn and Terborgh, 1979). In this species, wing-flashing by foraging males exposes white flanks on an otherwise dark body. Conspicuous wing-flashing might thus work as a highly visible recruitment signal for nearby species in the dark understory (Wiley, 1971). Contrary to expectation, dyeing the white flanks of males with black paint influenced neither the size of MSGs nor the duration of flocking (Botero, 2002). Despite negative results, this experimental approach is laudable because it puts to the test the idea that certain signals favor the formation and cohesion of MSGs.

If the presence of other species brings foraging benefits to the leader species, satiated leaders should be less inclined to produce recruitment signals. In the case of interspecific coordinated hunting in two fish species of the Red Sea discussed before (Sections 4.2.5 and 6.3.1), groupers initiated joint hunting forays by vigorous visual signals aimed at eels (Bshary et al., 2006). The production of such signals would be a good example of a flexible role in an MSG as groupers only behave in such a way in the presence of eels. Experimentally fed leaders produced no such signals, indicating that the purpose of the signals is most likely linked to the attraction of the other species. Experimental manipulations





**FIGURE 7.3 Attraction to vocal signals from leader species.** Playback experiments in a Sri Lankan rainforest revealed that non-leader bird species were attracted more often to the calls of putative leader species than to those of a non-leader species or silence. The attraction was stronger for insectivorous species than for omnivorous/frugivorous species. *Adapted from Goodale, E., Kotagama, S.W., 2005b. Testing the roles of species in mixed-species bird flocks of a Sri Lankan rainforest. Journal of Tropical Ecology 21, 669–676.*

of this sort are interesting because they directly address the putative value of signals made by leader species.

The experimental approach has also targeted vocal signals made by putative leader species. The principle behind this approach is simple: broadcasted calls or vocalizations made by a putative leader species should elicit approaches or interest from species known to associate with them in MSGs. This is the approach used by one of us (Eben Goodale) to determine which of the two species suspected to act as leaders was more attractive to other species in Sri Lankan MSGs (Goodale and Kotagama, 2005b). Nearby foraging species tended to approach the broadcast source more often after hearing calls made by the two leader species than those made by a non-leader species or following silence, which strongly suggests that calls alone can attract other species and be a facilitating factor in the formation of MSGs (Fig. 7.3). Interestingly, it was the combination of calls from the two putative leader species rather than calls from either species alone that proved the most attractive. Other experimental studies also showed that vocal signals can attract nearby species in bird MSGs (Mönkkönen et al., 1996; Goodale et al., 2012; Suzuki, 2012; Cordeiro et al., 2015) and also in monkey MSGs (Cords, 2000; Windfelder, 2001).

The above studies are useful to determine whether vocal signals can attract other species. They do not address what happens after the species have aggregated. After aggregation, other signals alongside vocal cues could play an

important role in maintaining cohesion. It is also important to consider the possibility that calls from another species elicit interest because they are perceived as a challenge to defended resources rather than as a signal to form an MSG. This hypothesis is more easily dismissed when joining species are not territorial. Overall, the main advantage of playback experiments is that attraction to another species can be separated from attraction to particular food patches, which could be associated with the presence of that species.

The playback approach can also be used to investigate whether calls made by leader species possess features that are especially attractive to other species. In the Sri Lankan rainforest groups mentioned earlier, the racket-tailed drongo, a leader species, benefits from the presence of food-flushing species. Drongos are also known to mimic calls from other species. It turns out that playbacks of drongo calls with more mimicked elements proved more attractive to other species (Goodale and Kotagama, 2006). Calls with more mimicked elements might give the impression that more species are present in the habitat. Whether mimicry has evolved to play that purpose is not known (Section 6.3.3).

### 7.2.2.3 Null Models

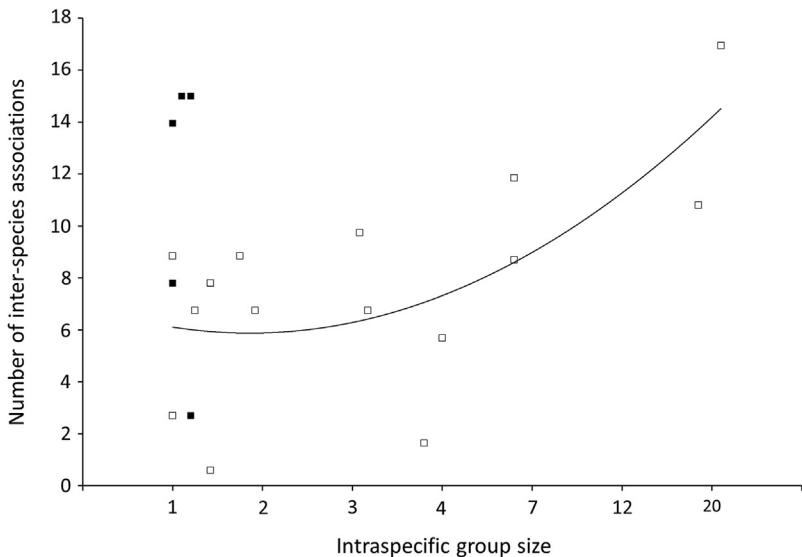
Fitting species into specific roles in an MSG works best when a species almost always leads or follows. In less black and white cases, leadership can be variable and depend on a host of factors such as species composition (Diamond, 1987) or habitat type (Morse, 1970; Gram, 1998). Despite its shortcomings, the indices developed by Morse (Section 7.2.2.1) provided a way to measure leadership on a continuous scale. Leader species would occur at one end of the continuum and follower species at the other end. The challenge now is to develop a continuous measure of leadership that takes into account the availability of other species in the habitat. The use of null models, which can specify how often different species are expected to cooccur by chance in an MSG, allows us to classify a species according to its degree of association with other species. A leader species would be expected to have stronger ties with other species or to occur with other species more often than expected from a null model of random associations among species.

Recent work tackled this issue by using data from avian MSGs in lowland tropical forests of India (Srinivasan et al., 2010). The idea was to compare the observed pattern of cooccurrences between pairs of species to that expected under a null model of cooccurrences. A large positive deviation from the expected value would suggest that a species is more nuclear or plays a more central role in MSGs. In this tropical system, many species cooccurred at levels well above the null expectation, which suggests that particular species sought one another.

The number of interspecies associations above this null expectation can be used as a continuous measure of nuclearity, which can then be related to various ecological factors believed to be associated with nuclear species. In

particular, the number of interspecies associations positively correlated with the intraspecific group size of a species (Fig. 7.4), which supports the idea that a nuclear species is more gregarious (Moynihan, 1962). For one type of flock in this system, the number of interspecies associations was also larger for sallying species than for gleaning species. Sallying species are often believed to act as sentinels in MSGs because they actively scan their surroundings for prey and can incidentally detect predators more easily (Wiley, 1971; Munn and Terborgh, 1979). This study thus provides support for the hypothesis that sallying species are attractive to other species although in fairness the association could run the other way if sallying species seek other species to obtain food.

One drawback of the methodology just described is that the nuclearity index is study-dependent: the number of interspecies associations must be a function of the number of available species, which might vary across study systems. This makes it difficult to compare the index across studies or ecological conditions. A further issue is that in systems with a large number of species, some species are likely to be closely related. As such, they might share similar tendencies to lead or follow, in which case their nuclearity index values might be quite similar and nonindependent. Inertia in nuclearity index values caused by relatedness would be an issue of statistical concern in such analyses. Finally, the nuclearity



**FIGURE 7.4 Gregariousness and interspecific association patterns.** In understory avian mixed-species groups of lowland tropical forests in India, species that tend to associate more often with other species than expected by chance also tend to occur in larger groups. Sallying species in these flocks (*black squares*), which scan the surroundings for aerial prey, are distinguished from gleaning species (*open squares*). Adapted from Srinivasan, U., Raza, R.H., Quader, S., 2010. *The nuclear question: rethinking species importance in multi-species animal groups*. *Journal of Animal Ecology* 79, 948–954.

index does not address the issue of leadership per se, that is, whether a species actually leads others. It is quite clear that a species must cooccur more than expected by chance with other species to act as a leader.

Null models have also been used to address the issue of leadership more directly. In groups composed of two species, it is quite reasonable to expect that at least one of the species benefits from the association. A null model for the composition of groups composed of two species was formulated using the occurrence of gregarious and nongregarious species in tropical evergreen forests of India (Sridhar and Shanker, 2014a). As it turned out, gregarious species occurred disproportionately more often in two-species groups than expected by chance. Observations of such groups in the field also revealed that the gregarious species led more often than the others. Nuclear species in fish are also known to occur in intraspecific groups, and the approach developed here for birds could be used to determine whether associations including gregarious species of fish occur beyond the level expected by chance (Sazima et al., 2007).

Null models can be seen as a first step to identify associations between particular interacting species that occur above the level predicted by chance. Once nonrandom associations are identified, the purported benefits of such associations can be sought and perhaps related to specific roles in groups (Srinivasan and Quader, 2012). Spatial and temporal changes in the strength of these associations can also be used to infer benefits, as has been done recently in MSGs of large East African mammals (Kiffner et al., 2014).

#### 7.2.2.4 *Social Network Analysis*

At its very core, MSGs represent a collection of individuals from at least two species that interact at a rate that exceeds what would be predicted by random encounters in the same habitat. If some species lead such groups, we would expect such species to be at the core of these groups, that is, they would be involved in many more associations with other species than predicted by chance. The null model approach presented earlier allows us to quantify such associations, but this method gives the same weight to all nonrandom associations by simply culling the number of associations above the random level. What we need is a tool to map out relationships between all individuals of all potentially interacting species in a specific area during a specific time period. Metrics from such a network of interacting individuals could be derived to determine not only the number but also the strength of interactions among individuals and species. Clusters of individuals from a particular species might become apparent in the network, which could be linked to particular roles in the group.

Social network analysis provides just this sort of tool (Croft et al., 2008). Social network analysis records associations or interactions between different individuals from different species over a fixed period of time in a particular habitat or location. The collective links between individual and species nodes constitute the social network. Metrics have been developed

to characterize such networks, which allow us to get a quantitative estimate of the sociality of an individual and of the species in general in such a network. For instance, individuals or species that form the core of a group would be expected to have a high “centrality” value as they are involved in more associations. Such estimates can be compared for different species and across ecological conditions (Wey et al., 2008). Returning to the study where leader species were experimentally removed from woodlots (Dolby and Grubb, 1999), the social network analysis of species interactions before and after the manipulation would provide the quantitative estimates necessary to statistically compare the two situations.

Social network analysis can be applied to interactions between individuals from just one species (Lusseau, 2007) or to interactions between individuals of several species in the same habitat. As an example, the network of interactions between an introduced species of fish in a novel habitat and local species was drawn to highlight the potentially disturbing consequences of the invasion in terms of relationships between native species (Beyer et al., 2010). Social network analyses of interactions between species that can actually form groups together are of particular interest for our purpose.

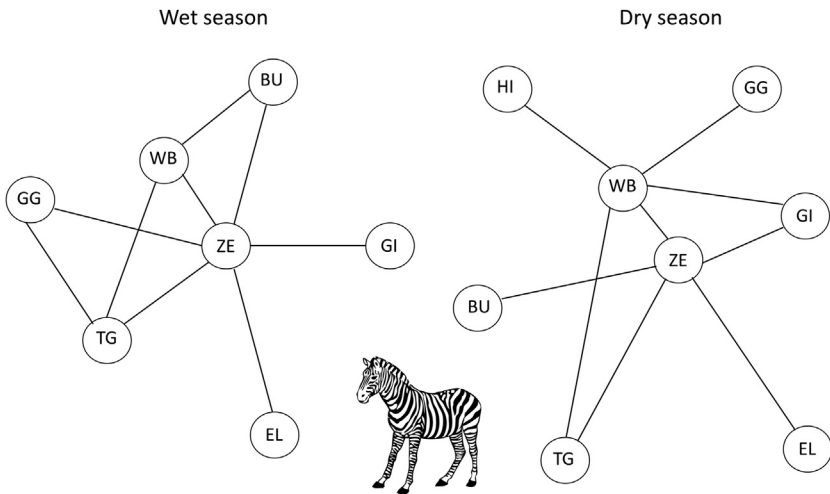
Social network analysis carried out at the level of the individual requires individual identification. In many field situations involving MSGs, individual identification is not possible given the large pool of interacting individuals or their distance from the observer. In such cases, the social network analysis can be carried out at the species level (Sridhar and Shanker, 2014a). However, it is clear that any variation in association strength within species will be missed. This is important because we often think of a species in an MSG as having fixed attributes, while it is often the case that substantial variation can occur among individuals of the same species. For instance, in MSGs of tit species interacting at feeders, larger individuals tended to have more associates than smaller ones, perhaps reflecting the fact that subordinate birds try to avoid others (Farine et al., 2012). An analysis carried out at the species level would not be able to identify this trend, if dominance acts mostly within rather than among species.

Recent applications of social network analyses to MSGs have been able to shed new light on species roles in groups. In East Africa, large browsing mammals often congregate in MSGs (FitzGibbon, 1990; Burger and Gochfeld, 1994; Pays et al., 2014; Schmitt et al., 2014). Earlier studies focused on the costs and benefits that some of these species experience in MSGs ([Chapters 4 and 5](#)), but species differences in attractiveness to others and whether the structure of these groups varies across ecological conditions were not addressed until recently.

Abundance estimates of species occurring along stretches of roads in two ecosystems in East Africa allowed researchers to establish whether some species occurred more frequently than expected by chance in MSGs and whether some species played a more central role in these associations (Kiffner et al.,

2014). In particular, plains zebras tended to be involved in many more associations than expected by chance and showed strong patterns of cooccurrences with other species, especially wildebeest (Fig. 7.5). Associations weakened during the dry season, perhaps in response to a decrease in food availability, which would reduce the benefits of foraging closely with other species. Another study showed that zebras decreased their vigilance in the presence of wildebeest, a species that is preferred by their common predator, the African lion (Schmitt et al., 2014). Such benefits might explain why zebras and wildebeest are so strongly associated and suggest that zebras might seek other species to reduce predation risk.

Social network analyses have also focused on MSGs in other species including birds and even bats (Ancillotto et al., 2015). In thornbill flocks in Australia, the analysis revealed again the central role of putative leader species (Farine and Milburn, 2013). In addition, each individual was marked with a distinctive series of color leg bands, and it was possible to see that females had different social connections than did males. Other studies contrasted the structure identified by social network analysis between different geographical areas (Sridhar et al., 2013) and over several years and across environmental conditions (Anguita and Simeone, 2015).



**FIGURE 7.5 Social network analysis of East African mixed-species groups (MSGs).** Browsing mammals in the Tarangire–Manyara savannah ecosystem in East Africa aggregate in MSGs in which plains zebra play a central role. The strength of the association between pairs of species is negatively proportional to the length of the bar relating each species. In the dry seasons, associations became noticeably weaker (BU, cape buffalo; EL, eland; GG, grant's gazelle; GI, giraffe; HI, hippopotamus; TG, Thomson's gazelle; WB, wildebeest; ZE, plains zebra). Adapted from Kiffner, C., Kioko, J., Leweri, C., Krause, S., 2014. Seasonal patterns of mixed species groups in large East African mammals. *PLoS One* 9, e113446.

As with null models, social network analysis cannot reveal which species is actively responsible for the formation and cohesion of MSGs. However, it provides a means to identify key species or individuals in such groups. Quantitative indices produced by social network analysis can be used to test hypotheses about the factors driving the formation of MSGs.

### 7.2.3 Characteristics of Leader Species

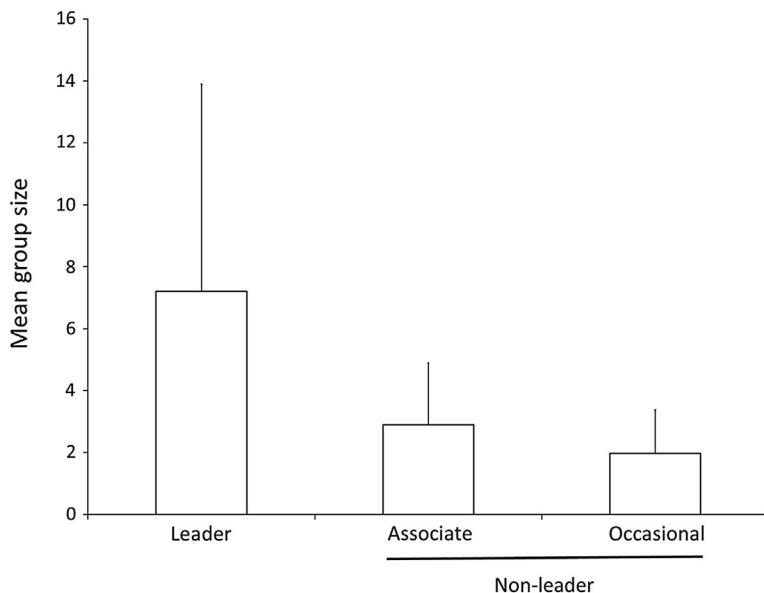
Several traits by leader species are believed to play an important role in the formation and cohesion of MSGs. In the following, we identify such traits in different taxa.

Following the publication of Moynihan's scheme to classify the role of species in MSGs, avian researchers routinely reported whether some species in their study system tended to be nuclear. Compiling findings from many study systems, they made it clear that in birds many characteristics occur frequently in leader species. Specifically, these species have a high propensity to occur in such groups, form intraspecific groups, and are often conspicuously active and vocal (Hutto, 1994). Level of activity is quite subjective and might be hard to assess empirically. But the relationship between leadership and gregariousness is much easier to determine by simply measuring intraspecific group size.

Why would gregariousness be an asset for leader species? A large group size could simply increase visual conspicuousness, making it easier for nearby species to join and follow the leading species over time and through space. Noisiness associated with frequent contact calls in a large group could also ease detection from afar. Other traits might also be associated with group size and further facilitate flocking. Conspicuous alarm calling, perhaps selected for when there are large groups of related individuals (Maynard Smith, 1965), might act as a cue to locate the leader species, rallying other species rapidly to maintain group cohesion (Goodale and Kotagama, 2005b).

In a survey of Neotropical avian groups, Powell reported that group size tended to be slightly larger in leader species than in those that typically follow (Powell, 1985). Two of us (Eben Goodale and Guy Beauchamp) extended this analysis to a much broader range of study systems worldwide (Goodale and Beauchamp, 2010). Avoiding circularity is important in such an endeavor because leadership is often defined by a large group size. We thus looked for evidence of leadership independent of group size. Leader species often occur at the forefront of groups and initiate more movements than the others. We might expect gregarious species to lead flocks simply because they outnumber other group members. In this sort of random model, it would be unlikely to consistently find all members of the leader species at the forefront of the group.

We contrasted mean flock size across different types of species in each study system: the leader species, one associate species (a species commonly found in such groups, but not a leader), and in one occasional species (occurring in less than 50% of the groups). In our worldwide survey, mean group size was indeed



**FIGURE 7.6 Leadership and intraspecific group size in avian mixed-species groups (MSGs).** A worldwide survey of various MSGs in birds revealed that mean intraspecific group size was larger in species that led groups than in non-leader species, including those that are commonly found in groups but do not lead (associate) and those that occur less frequently in groups (occasional). Means and standard deviations are shown. After Goodale, E., Beauchamp, G., 2010. *The relationship between leadership and gregariousness in mixed-species bird flocks. Journal of Avian Biology* 41, 99–103.

significantly larger in leader species than in associate and occasional species from the same groups (Fig. 7.6). Such differences in intraspecific group sizes between nuclear and attendant species might also hold in fish MSGs, but this has not yet been analyzed rigorously (Lukoscsek and McCormick, 2000).

In another worldwide survey of MSGs in birds, Sridhar et al. (2009) found that cooperative breeding was more common in leader than in follower species. Cooperative breeders often live in kin groups (Cockburn, 1998), so again we might expect well-developed communication and alarm signals in such groups. Such signals could be eavesdropped on by other species to increase their safety. However, further study is required to identify the exact traits and behaviors associated with cooperative breeding that actually help to promote MSGs in birds.

Leadership has also been addressed in different species of tamarins that often form MSGs in tropical forests of South America. Here, dominance status appears to influence leadership, as the smaller species in the mostly two-species groups formed by these monkeys typically leads (Terborgh, 1983; Peres, 1996; Smith et al., 2003). Leadership probably increases the chances of accessing resources before the more dominant species can monopolize food patches. Dominance



status in MSGs also affects leadership in dolphins (Qu  rouil et al., 2008) and in fish (Lukoschek and McCormick, 2000; Sazima et al., 2007).

The production of calls appears to serve as a signal to facilitate the formation of MSGs in tamarins (Pook and Pook, 1982) as well as in many other species of primates (Cords, 2000). What is not known is whether the production of calls or the particular attributes of these calls are different in leader and non-leader species and whether these calls are specifically targeted at other species or are simply made to attract conspecifics and heterospecifics alike.

### 7.3 SENTINEL BEHAVIOR

In several species of birds and mammals, and even in fish, vigilance against predators can be coordinated at the group level (Bednekoff, 2015). In such groups, high vigilance maintained by one or a few individuals allows other group members to focus their attention on other activities (such as resting or foraging). This sort of vigilance is also often carried out from vantage points providing a better view of the surroundings. Coordination of vigilance at the group level and selection of vantage points to carry out vigilance characterize sentinel behavior (Bednekoff, 2015).

Sentinel behavior has been noted very early on by naturalists (Wallace, 1875; Cary, 1901; Elliott, 1913). In *Chacma* baboons, for instance, Elliott (1913) noted that one or a few individuals located on a prominent rock warned the rest of the foraging group about impending danger. Sentinel behavior has typically been investigated in single-species groups, but recent studies show that its occurrence in MSGs is not rare and might in fact be a force that favors the formation and cohesion of such groups.

Coordination of vigilance represents a hallmark of sentinel behavior in single-species groups. In a coordinated group, individuals take turns to perform vigilance; which implies that vigilance is maintained at a stable level over time. As far as we know, coordination of vigilance between species has not been documented in MSGs. In most cases, one species takes advantage of the higher vigilance provided by another species without reciprocating.

In an MSG, a sentinel role can be attributed to species that perform a disproportionate share of the vigilance and that can warn other species more rapidly or effectively than would be the case if the other species maintained vigilance on their own. For this purpose, sentinel species tend to provide frequent and conspicuous alarm calls. Based on these traits, sentinel species have been identified in many MSGs in birds and in mammals (Table 7.2).

High vigilance in a sentinel species has been related to several factors including foraging technique, vantage position, large individual size, and large group size. In terms of foraging technique, sallying species, as noted earlier, tend to scan their surroundings to a greater extent when searching for prey, which might incidentally facilitate the detection of predators. Large size might be useful to get a better view of the surroundings. A large group size increases the chances

**TABLE 7.2** Cases of Sentinel Behavior in MSGs of Birds and Mammals

System	Sentinel Species	Attributes of the Sentinel Species	References
<b>Birds</b>			
North American scrubland	Pinyon jay	High position	Balda et al. (1972)
Peruvian understory	Bluish-slate antshrike	Sallying	Munn and Terborgh (1979)
Peruvian canopy	White-winged shrike-tanager	Sallying	Munn and Terborgh (1979)
European heathland	European stonechat		Greig-Smith (1981)
North American temperate forest	Black-capped chickadee		Sullivan (1984)
Brazilian savannah	White-banded tanager	High position	Alves and Cavalcanti (1996)
Brazilian understory	Cinereous antshrike		Stouffer and Bierregaard (1996)
Brazilian savannah	Chalk-browed mockingbird	Large group size	Ragusa-Netto (1997)
Brazilian understory	Black-goggled tanager	Sallying	Maldonado-Coelho and Marini (2000), Maldonado-Coelho and Durães (2003)
Brazilian savannah	White-rumped tanager	High position	Ragusa-Netto (2000)
Taiwanese forest	Grey-cheeked fulvetta	Large group size	Chen and Hsieh (2002)
Sri Lankan understory	Greater racket-tailed drongo	Sallying	Goodale and Kotagama (2005a)
South African savannah	Fork-tailed drongo	Sallying	Morgan et al. (2012), Baigrie et al. (2014)
Tanzanian forest	Square-tailed drongo	Sallying	Cordeiro et al. (2015)
<b>Mammals</b>			
African savannah	Grant's gazelle	Large size	FitzGibbon (1990)

**TABLE 7.2** Cases of Sentinel Behavior in MSGs of Birds and Mammals—cont'd

System	Sentinel Species	Attributes of the Sentinel Species	References
Ivory Coast forest	Diana monkey	High position and large group size and spread	Bshary and Noë (1997)
South American forest	Moustached tamarin	High position	Heymann and Buchanan-Smith (2000)
Ivory Coast forest	Diana monkey	High position and large group size	Wolters and Zuberbühler (2003)
South African savannah	Meerkat	High position and large group size	Waterman and Roth (2007)
<b>Birds–Mammals</b>			
East African desert	Von der Dercken's and Eastern yellow-billed hornbills	High position	Rasa (1983)
South African savannah	Fork-tailed drongo	High position	Sharpe et al. (2010)
<i>MSGs, mixed-species groups.</i>			

of detecting threats by adding more eyes and ears to the detection of predators. Similarly, vantage positions such as the top of trees can increase detection distance. Alarm calling might be more frequent in sentinel species because of higher vigilance, but other factors can predispose such species to be more vocal. As noted earlier, many sentinel species are also cooperative breeders, which are suspected to produce more frequent and elaborate alarm calls. In addition to frequent alarm calls, some sentinel species also produce calls to attract other species (Goodale and Kotagama, 2006; Baigrie et al., 2014; Goodale et al., 2014). Whether sentinel behavior in an MSG constitutes a flexible or fixed role is not clear. In many cases, the sentinel species appears to play this role involuntarily; it simply reflects its tendencies to produce more alarm calls or to occupy a better position for antipredator vigilance. For instance, the Diana monkey in tropical forests of Africa lives in large groups and typically forages high in the trees. This species is thus more likely to raise the alarm than other species foraging in

smaller groups at lower strata (Bshary and Noë, 1997; Wolters and Zuberbühler, 2003). Alarm calling in this species appears aimed at conspecifics (or predators) (Zuberbühler et al., 1997), and there is no indication that alarm call features are any different when this species forages in MSGs. There is also no indication that different species in such groups coordinate their vigilance.

Perhaps the best evidence for a flexible role in sentinel species comes from MSGs where the sentinel species also forages alone, in which case particular features of sentinel calls or behavior can only be related to the occurrence of other species. Deceptive alarm calling and the use of calls to attract other species can be seen as features that evolved in the context of MSGs. For instance, when they forage alone, fork-tailed drongos, a bird species that often associates with other species in South African savannah (Section 5.4.5), give alarm calls after detecting aerial predators but tend to ignore terrestrial predators (Ridley et al., 2007). When joining another species that forages on the ground, the drongos also provide alarm calls after detecting terrestrial predators that cause a threat to the individuals below. Other work shows that drongos can mimic the calls of other species to attract other species to form MSGs and also to acquire resources deceptively (Goodale and Kotagama, 2006; Baigrie et al., 2014; Flower et al., 2014; Sections 6.3.2 and 6.3.3).

## 7.4 CONCLUSIONS

Roles in MSGs have been related to leadership and sentinel behavior. We have reviewed several procedures to identify leaders in MSGs. The use of more objective tools to assess leadership is a welcome development that will surely help to clarify the various roles played by different species. Leaders and sentinels have now been documented in many MSGs in fish, birds, and mammals.

In many cases, roles coopt particular attributes of a species with seemingly little adjustments to the multispecies context. In terms of leadership, for instance, we lack evidence that the larger groups of leader species evolved to attract other species more effectively. Large groups, instead, might simply reflect selective demands for foraging in single-species groups. Similarly, frequent and more elaborate calling by leader species could reflect evolution for the benefit of kin in cooperative breeders.

The best evidence for flexible roles in MSGs comes from studies in which leader or sentinel species use specific signals to attract or deceive other species. This was the case for groupers using a signal to entice eels to form hunting groups. This signal was only used when groupers were hungry and was not aimed at other groupers (Bshary et al., 2006). Alarm calls by sentinel species tailored to a multispecies context (Goodale and Kotagama, 2006; Ridley et al., 2007; Flower et al., 2014) or the use of deceptive alarm calls by sentinel species (Munn, 1986; Baigrie et al., 2014) also strongly suggest that sentinel species actively respond to the presence of other species in their groups.

Future work could focus on visual or vocal signals produced by leaders and sentinel species to determine if specific features of these signals facilitate the formation or cohesion of MSGs. In addition to group size, Moynihan predicted that other features of leader species could play a role in birds, including their coloration (Moynihan, 1960). Signal convergence in MSGs, whether learned or acquired through evolution, might also be expected to facilitate communication in such groups (Diamond, 1981; May-Collado, 2010; Beauchamp and Goodale, 2011).