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Follow me! I'm a leader if you do; I'm a failed initiator if you don't?

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Leadership is arguably one of the most important themes in the social sciences, yet until recently has been largely overlooked in the natural sciences (Dyer et al., 2009; King et al., 2009; Van Vugt, 2006). In fact, search for articles on the topic of "leadership" on the ISI Web of Knowledge and it will return nearly 5500 psychology related articles, but less than 500 in the disciplines of ecology, zoology, and behavioural science.[1]

The difference in the volumes of research in each field is largely a consequence of the contexts in which leadership is studied. In the social science literature, the study of leadership is vast and questions are asked concerning political, commercial, educational, environmental and moral leadership. In contrast, for natural scientists, interest in leadership has arisen as a consequence of researchers asking questions about collective movements. For example, how does a group of individuals decide *when* to move? Or, how does a group decide *where* to move? When beginning to tackle such questions we first see the outcome: an individual at the front of a group progression, moving in a particular direction, with group-mates following closely. It is therefore little surprise that 'leadership' has become a feature of studies of collective movements and a number of different definitions exist. I like Krause et al.'s (2000) definition of leadership – as the initiation of new directions of locomotion by one or more individuals which are then followed by other group members. One problem with such a definition (and any others I can find) is that our focus remains on the outcome, i.e. a successful movement where all individuals in a group depart together. 'Failed' group movements where a move attempt is cancelled, and the group remain in their default 'state' are seldom considered (see Gautrais, this issue for a discussion). This is important, because to understand how leaders and followers emerge (or are born, or are made) we must consider why movements of some individuals are not followed – the failed initiations.

Petit and Bon (this issue) suggest that the concept of leadership and the use of the term itself are 'misleading' (very nice pun!) when used in a biological context, and rather suggest that we adopt the term 'initiator' when we talk about specific individuals initiating a collective departure. Their argument is based on a premise that an individual can more appropriately be described as a 'successful initiator' when their actions elicit a collective movement from the entire group to which they belong, and an 'unsuccessful initiator' when they do not. Given that leadership *implies* followership, is suggestive of a specific social role (which I will come to later), and the term 'unsuccessful leader' appears to be somewhat an oxymoron, Petit and Bon argue that the concept of leadership in limits, or at least confuses, our understanding of collective movements.

I do agree that leadership can conjure up (sometimes unhelpful) assumptions in one's mind when it is discussed in the context of collective movement. Nevertheless, when individuals follow another's actions, they make that individual a leader, and this is a concept that is mirrored at many levels of social interaction. In species where individuals are better off acting and moving together (Krause and Ruxton, 2002) leader–follower patterns are likely to emerge not

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only during coordinated group movements, but also during social foraging, deterring predators, teaching, and dealing with intra- and inter-group conflicts (King et al., 2009; Van Vugt et al., 2008). Across these different contexts, individuals may initiate a group action – and lead – from the front, or the back, in small groups, or in large groups, and this does not necessarily need to be imposed 'top down' (Barelli et al., 2008; Kummer, 1995; Piyapong et al., 2007; Sumpter, 2009). Indeed, rather than directing group-mates like an army drill sergeant, individuals may assume leadership roles based on relative differences in motivation, experience, or personality (see King et al., 2009 for a review). Leadership and followership can therefore be a passive process, where individuals adopt leader and follower roles and self-organise without explicit communication or understanding of one another's roles (e.g. Couzin and Krause, 2003; Couzin et al., 2005). Improving our understanding of leader–follower interaction patterns across these many contexts can inform us greatly on the evolution and maintenance of sociality (Wilson, 1975). Using the term leader and follower will also facilitate the study of fundamental shared principles within and across disciplines, and allow us to identify, describe, and understand situations when "the behaviour of one or a few individuals steers the behaviour of many" (King et al., 2009).

1. Getting started

To illustrate the almost inevitable emergence of leaders and followers where groups need to coordinate their movements, let me re-tell an anecdote that I have used elsewhere (King et al., 2009). Imagine a pair of hungry individuals that have to stick together for protection and have to choose between two available food patches – patch A or patch B – and these patches are of exactly the same size and quality. Whichever individual makes the move to patch A or B first, will leave the other individual no option but to follow. Since they get the same food reward at each food patch, a failure to coordinate their behaviour and to move together will mean they forfeit the reduced risk of predation they gain from sticking together.

With such coordination problems, any trait that increases the likelihood of one individual moving first will make them more likely to emerge as the leader. More formal theoretical analyses exploring similar coordination problems using dynamic game-theoretic models shed light on what these 'traits' might be. Rands et al. (2003) suggested that individuals in foraging pairs should follow a simple rule-of-thumb: "if I'm hungry, I should forage; if not, then I should copy what my colleague is doing". In this case, being hungrier increases the chances of an individual becoming a leader. Subsequent individual-based modelling approaches have since explored the emergent properties of this rule-of-thumb in larger social groups (Rands et al., 2004), and the topic of state-dependent leadership is discussed elsewhere in this issue in greater detail (Rands, this issue; Fischoff, this issue).

More commonly, collective movements are difficult to achieve because individuals will have preferred directions or times to perform activities as a result of heterogeneity of interests due to sex, age, size or reproductive status. Realising coordination therefore results in unequal payoffs (Conradt and Roper, 2003, 2007), and there is an incentive for individuals to act as a leader and steer the behaviour of their group-mates toward their own preferred action. Under conflicts of interest, it is not difficult to envisage how leaders (i.e. successful initiators) may possess certain attributes making them attractive to group-mates and more successful in eliciting a collective movement (perhaps as a result of a lower propensity to give-up an initiation: Gautrais, this issue; Petit et al., 2009). These attributes can be identified examining the correlates of leadership and followership behaviour and the payoffs for adopting each role (King et al., 2008; Krause et al., 2000). In fact, understanding the relative payoffs to leading and following, and the similar or divergent goals of individuals involved, is a crucial aspect of studying collective movements.

2. How to study leadership and followership

Much of the recent work on collective movements has been to identify the rules that individuals in social groups employ when making the decision to go from a [collective] resting state, to a moving state. For example, Petit et al. (2009) studied the departures of captive capuchin monkeys (*Cebus capucinus*) between resting and foraging areas of their enclosure. They found that the collective departures were determined by (1) the frequency with which capuchins followed an individual that had proposed moving (the initiator), and (2) the propensity of the initiator to give up (i.e. cancellation rate). This cancellation rate appeared to be completely reliant on the number of followers an initiator attracted; if an initiator elicited more than three followers, the chances were the whole group would move. But if the initiator was unsuccessful in attracting three followers, or less, the chances are (s)he would give upon leading the group, and return to resting (they found no influence of individual initiator identity). This is an important contribution to our understanding of collective movements, and hints at fundamental shared mechanisms (in this case, quorum rules) across a variety of taxa (e.g. see Ward et al., 2008). However, it will be interesting to see if these results hold where the capuchin monkeys do not only have to decide when to shift between a single resting and feeding area, but when there are multiple foraging and resting locations, and where payoffs for individuals at each location differ. This would introduce conflict, and individuals would (if they were to stay together) have to decide both *when* and *where* to move simultaneously. Would we then see variability in the success of initiators, and the emergence of consistent leader–follower roles?

Early studies of collective movements conducted in the 1960s by Emil Menzel (reviewed in Menzel, 1974), highlight the role of how conflicting interests can mediate the emergence of leaders. In a series of experiments on captive chimpanzees (*Pan troglodytes*), Menzel assessed the extent to which a single 'informed' individual was capable of leading other 'naïve' group-mates toward a specific food source. Much like many modern day studies of leadership (e.g. Couzin et al., 2005; Dyer et al., 2008; Faria et al., 2009; Reebs, 2000) he studied the success of the informed individual controlling what he described as the nature and direction of group activity.

In the first set of trials, an established group of six chimpanzees were released from an indoor area into an outdoor enclosure. During experimental days the group was released with one individual having earlier been shown the location of a food item hidden within the outdoor enclosure. During control days the group was released with no individual having any knowledge of the location of the hidden food item. Unfortunately, only two of the six in the group were used as informed individuals, since these could be removed from the group easily and shown the hidden items with little aggression, but the results are intriguing nonetheless. In 40 out of 55 experimental days, informed individuals (irrespective of identity) led their group-mates directly toward the hidden food, and the group discovered the item within just a few minutes of being released. On control days, the group failed to find the hidden food on all but 1 day ($n = 44$) and did not attempt to search for food, except for the first few control days when the group ran to the location the food item was hidden on the previous day.

In a subsequent experiment, the two individuals in previous trials who were able to lead the group toward the hidden food sources

(let's call them 1 and 2) were shown hidden goals in different locations, that at times varied in quality (high preference fruits versus low preference vegetables). Menzel found that if both chimpanzee 1 and 2 were shown hidden items of the same quality (both shown fruit, both shown vegetables) a majority of the group would more often visit the location known to individual 1. Moreover, when individual 1 was shown fruit, and individual 2 a vegetable, the majority would follow individual 1 to the fruit (and this group would often include individual 2). When the reverse was true, individual 2 was less successful in eliciting a majority following to the more preferred food item, but still succeeded on at least half of the occasions. Overall, the group went to fruit over the vegetables on 21/27 trials.

In the first set of experiments, both individuals 1 and 2 could successfully initiate collective movements toward specific areas of their enclosures where only they knew food items were located. They were successful initiators (Petit and Bon, this issue), or leaders. When these previously successful initiators possessed conflicting information on the location of an equivalent food item, one individual emerged as more successful in leading the group to their known resource than the other. Despite the fact that this experiment is screaming out to be replicated today – so that we can test between cognitively demanding hypotheses, and those relying on relatively simple interaction rules – this early work serves to highlight one of the single most interesting aspects of leadership: Why was it that chimpanzee 1 was followed more often than chimpanzee 2?

Any individual can have higher motivation to perform a certain activity, but if (1) individuals have conflicting interests and (2) social and ecological pressures determine that *on average*, individuals experience enhanced fitness when acting as a group, then individuals will be faced with having to make choices to follow certain individuals and ignore others. Selection will therefore favour decisions to follow 'types' of individuals which result in group behaviours that result in higher individual payoffs.

3. Moving forward

To reiterate, individuals are more likely to initiate collective movements if they have a particular morphological, physiological, or behavioural trait increasing their propensity to act first and/or have a lower giving up propensity than their group-mates. Under conflict though, individuals are more likely to lead groups if they can attract an enthusiastic following. A number of recent studies examining the role of social dominance and personality types offer a platform on which we can develop this avenue of research (King and Cowlishaw, 2009).

In the case of social dominance, Sueur and Petit (2008) used network metrics to assess what rules may underlie follower behaviour in two macaque species: rhesus macaques (*Macaca mulatta*) and Tonkean macaques (*Macaca tonkeana*) that differ in the dominance styles: rhesus macaques are a highly hierarchical, whereas Tonkean macaques are egalitarian in nature. Sueur and Petit found that more dominant males often led collective movements in the hierarchical rhesus macaque, whilst there were no apparent correlations with leadership in the egalitarian Tonkean macaque. Understanding the interplay between dominance and leadership remains a challenge, not least because these terms are often used interchangeably in our daily life. Dominance can increase the probability of an individual acting first since it may be able to act more autonomously, whilst at the same time dominant individuals may be in a better position to elicit followership since they hold a particularly strong influence over the behaviours of group-mates and have an established importance within social networks (Krause et al., 2009; Lusseau, 2007). Dominants may also be able to enforce followership if they benefit disproportionately from a group activity (King et al., 2009). Yet, leadership does not necessarily go hand-in-hand with dominance, and further carefully designed studies adopting a comparative approach similar to that used by Sueur and Petit is surely the way to go.

In the case of personality, work on fish offers insight. In laboratory experiments with stickleback fish, Harcourt et al. (2009a) studied their ability of pairs of fish to coordinate excursions to foraging patches. Bold individuals tended to lead and explore new areas, while shy individuals showed strong follower behaviour. Most interestingly, they also discovered that an individual's leadership and followership potential was influenced by the behaviour of its partner; bold individuals enhanced shy fish joining tendencies whilst very shy individuals elicited greater leadership tendencies in their bolder partner. Studies of larger groups of fish (Magnhagen and Bunnefeld, 2009) and other species too (Kurvers et al., 2009), suggest a more influential role of bold individuals in group patterns of behaviour. This suggests the intriguing possibility that personality differences are maintained in populations through negative frequency dependent selection, and because they foster social coordination (Croft et al., 2009; Harcourt et al., 2009b). However, there is currently a lack of studies that explore the behaviours of individually marked (or tracked) animals in larger groups, and this would be necessary to test such ideas.

Dominance and personality are certainly not the only factors that we should consider. For instance, overlaying patterns of affiliate relationships to patterns of leadership and followership will also advance our understanding of the process underlying collective movements, and highlight the non-binary nature of collective patterns (Sueur et al., 2009). In fact, to tease apart the relative influence of these various traits – the labels we assign individuals based on their past behaviour – will allow us model the process, and then we are in a position to predict the outcome: when and where groups are likely to move. This in turn will not only provide insight to the evolution and maintenance of social behaviour, but inform conservation and management of social species and even the design of control mechanisms for autonomous grouping robots.

4. Misleading?

I began my contribution to this special issue with the intention of convincing researchers studying collective movements not to abandon the concept of leadership, but to look for it, describe it, and understand how it is that individuals are followed. This last point should not be underestimated; I whole heartedly agree with Petit and Bon that understanding failed initiations is crucial, but removing the concept of leadership, I believe, will not help. Where initiators elicit strong follower behaviour we can call these individuals leaders. What will be interesting – as we accrue more empirical data on collective movements – is how the temporal component to leadership will be incorporated into our definitions. Whether leaders act at a single movement scale or repeatedly over several movements is pivotal to defining an individual's contribution to group behaviour. Here, work on frequency dependence of behavioural tactics will surely offer insight (Giraldeau and Caraco, 2000; King et al., 2009). In sum, I argue that there is no problem with using the term leadership as long we provide an operational definition of what we mean by it.

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