The Anatomy of Leadership in Collective Behaviour

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Understanding the mechanics behind the coordinated movement of mobile animal groups provides key insights into their biology and ecology while also yielding algorithms for bio-inspired technologies and autonomous systems. It is becoming increasingly clear that many mobile animal groups are composed of heterogeneous individuals with differential levels and types of influence over group behaviors—often considered as “leaders”. The ability to infer this differential influence, or leadership, is critical to understanding group functioning in these collective animal systems. Due to the broad interpretation of leadership, many different measures and mathematical tools are used to describe and infer “leadership”, e.g., position, causality, influence, information flow. But a key question remains: which, if any, of these concepts actually describes leadership? We argue that instead of asserting a single definition or notion of leadership, the complex interaction rules and dynamics typical of a group implies that leadership itself is not merely a scalar quantity, but rather, a complex combination of many different components. In this manuscript we develop an anatomy of leadership, identify several principle components and provide a general mathematical framework for discussing leadership. With real and synthetic examples we then illustrate how to use this framework. We believe this multifaceted approach to leadership definition will allow for a broader understanding the role of leadership and its inference from data in mobile animal groups and beyond.

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Whether observing a herd, a swarm, a school, a flock, a pack, or any collective motion of animal groups, an immediate question is, what is the leadership structure? Who is in charge and who is following, and does such structure stay the same or change over time? Despite the central importance of understanding leadership structure in group behaviors, there is surprisingly little explicit mathematical description beyond recent work associating leadership roles with the inference of coupling structure according to (predictability) causality measures such as Granger causality, transfer entropy, and causation entropy. Our main contribution of this work is the development of an anatomy of leadership as a formal language to describe the many aspects of leadership.

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that a direct momentary snapshot observation will likely miss. The broad interpretation of leadership goes beyond measurements associated with just predictability (the information flow based causation measurements), to potential aspects and aspects associated with various triggering stimulus, we hope will greatly enrich the study of the dynamic roles individual animals play toward the success of the group. While we have suggested several primary aspects of leadership types and forms, such a list is by no means exclusive. Rather, we view this as a preliminary taxonomy of primary (or “principle”) behaviors, together of which are necessary to adequately characterize the complex behavior of a collective animal group. We expect over time other principle behaviors may be identified but perhaps associated with our broader concept of anatomy of leadership.

I. OVERVIEW

Mobile animals groups (e.g., flocks, herds, schools, swarms) are ubiquitous in nature. In such collective systems, the interactions between individuals may be as important as characteristics of the individuals themselves. Insight into these interactions and their impact on the group dynamics is of fundamental importance for our understanding of both the ecology of these systems as well as design and control principles underlying general complex systems.

A key challenge in the study of collective animal behavior is understanding how groups of organisms make decisions as a whole, for example about where or when to go. Group decision-making processes range from despotic to shared, although even in systems with shared or distributed decision making there are likely inter-individual differences (e.g., sex, rank, personality, size, nutritional state, informational state) that produce asymmetry in influence. Models suggest that such heterogeneity is potentially important to group-level dynamics, but inferring differential influence and leadership from empirical data, though often attempted, is an open challenge. As we elaborate in some detail in this paper, a key step toward tackling this challenge lies in the recognition that the notion of leadership is not merely a simple, unidimensional concept. Instead, a rich palette of different types and forms of leadership often coexists, even for the very same system. Thus, we argue that a precursor step to the “correct” inference of leadership is the clarification of what (type of) leadership is sought of, which is the central goal of this paper. Without such, any inferred leadership can potentially be deemed inappropriate.

The need to distinguish between the definition and inference of leadership is standing out as a central problem partly because of the acceleration of technical progress that enabled collection of “big” data. For example, new technologies to collect the simultaneous trajectories of all members of a mobile animal group, along with increases in computing power, make the near future a fruitful time to meet this challenge. Will having large amount of real-world data alone be sufficient to address questions about leadership, or do we (still) need conceptual advances? As recently reviewed by Strandburg-Peshkin et al., most efforts to infer leadership have used position within a group (e.g., leaders are assumed to be at the front), initiator-follower dynamics or time-delayed directional correlations. Information theoretic measures provide additional, potentially more powerful and less subjective, tools to infer leadership and influence. However, as we discuss in Section II, a central viewpoint of this paper is that any measurement of leadership needs to start by clarifying the particular type or form of leadership one is after. Without such clarification, the “leadership” resulted from the application of any inference method can be subject to misinterpretation, and perhaps more seriously, lead to fundamentally flawed conclusions about
the interaction mechanisms of an animal system.

To illustrate the many facets of leadership and thus the need to distinguish between its definition and measurement, consider, for example, the case of migrating caribou. Older, more experienced individuals are thought to guide the migration-scale movements \(^{27}\), however, pregnant or nursing females might have increased nutritional requirements \(^{28}\) and thus guide movements along that path towards habitat with better forage opportunities \(^{29}\). Thus who is leading depends on the time- and length-scale of the movements considered. Additionally, for some populations fall migration coincides with the rut, so mating behaviors drive social interactions: a dominant male may attempt to herd females or drive other males away. Such a male is certainly influential, but perhaps should not always be considered a leader, at least in the context of the migration. Finally, whether or not an individual is a leader might depend on who one or which group is considering as a potential follower. A nursing (and thus infertile) female might be ignored by the libidinous male, but will be closely followed by her calf \(^{30}\). Because there are many scales and types of influence/leadership one should begin such explorations with a clear question and select analytical methods to match.

To reiterate, the central goal of this paper is to develop a framework for defining and (potentially) inferring different types of leadership, thus offering a practical guidance for researchers hoping to match questions about leadership and influence with the appropriate methods and potentially avoid pitfalls. We hope that the combination of mathematical rigor, biological intuition, together with several real and synthetic examples will make our framework accessible and interesting to both biologists and applied mathematicians. Section II gives a brief introduction to this subject area and related work. Section III outlines on a conceptual level what we believe to be the fundamental components of leadership in mobile-animal groups. In Section IV we construct a sandbox of leadership where we provide several model examples of leadership in order to categorize and project each example on to components of Section III.

II. CAUSAL INFORMATION FLOW, INFLUENCE AND LEADERSHIP

Before diving into the technical details and interpretation of what is leadership and how to measure it, in this section we discuss a few related concepts including information flow and influence. Although these concepts are sometimes used as ways to infer leadership in the existing literature, we take a different perspective to view them as related (but not identical) to the notion of leadership.

Information theory provides sophisticated measures for rigorously quantifying concepts like “the reduction in uncertainty about the present state of X given past states of Y.” As such, these measures are often associated with concepts like information flow, causality, influence and even leadership—and often all of these terms are used interchangeably. These measures are often viewed as less subjective inference methods because almost no assumptions need to be made about the structure of the system being observed. As a result, information theory has become a popular tool for inferring leadership from time series \(^{19–26,31}\). However, while influence, information flow and causality are all closely related to the notion of leadership, as we elaborate in this paper, these concepts are inherently different and therefore are not readily interchangeable. Furthermore, recent work has begun to show that these information measures fail to even capture information flow \(^{32}\) let alone leadership.

The following section discusses the inherent differences between information flow, causality and influence and provides motivation for why we do not believe any of these alone fully quantifies leadership. For a reader only interested in the anatomy of leadership and not the motivation the remainder of this section can be safely skipped.

Information flow and entropy, as we have contented in previous mathematical works \(^{24,33,34}\),
is a fundamental concept in coupled (dynamical) systems, and the associated stochastic processes. Information theory, as formulated upon Shannon entropy and its variants, basically describes the average “surprise” one should attribute to observing a specific value or state of a random variable. More formally, such quantification of surprise or (un)predictability is referred to as “entropy” and can be defined rigorously as a function of the underlying probability distributions. When the time evolution of multiple variables are considered, the state of a variable often depends on the history of a set of related variables, and such inter-variable dependencies can be viewed as “information flow”. Explicit characterization of information flow in coupled systems can be done by quantifying how informative (again as a notion of surprise) one should be in measured observations conditioned on given previous observations, giving rise to commonly used measures such as transfer entropy and causation entropy. In other words, information flow describes the reduction in uncertainty regarding forecasts for predictions associated with conditioning on the past in various combinations. Thus whether by Granger causality, transfer entropy, causation entropy, or some other method, the idea is to ask if there is a reduction in uncertainty with knowledge of the past of a perhaps coupled variable. Clearly, this question is universally relevant from a wide range of scientific fields of science or mathematics. However, part of the theme of this paper is that these information flow concepts themselves are not sufficient or equivalent as leadership.

Causation is a related but not identical concept as information flow. The notion of causality has many interpretations, depending on the context, from philosophical, statistical, to dynamical. Here we will avoid the philosophical direction entirely, but note that some of these do coincide with the others. Statistical perspectives are sometimes relevant to a stochastic process, especially from the influential work of Pearl, associated with a calculus for understanding interventions, but not always relevant to our context. We are more so interested in understanding interpretations of causal influence, of a free running system, that is, a system that is passively observed rather than actively probed. As such, this relates more closely, almost synonymously to the concepts of information flow in a stochastic process, but not quite identically. We take the same perspective as Granger in his line of reasoning that eventually lead to the 2003 award of the Nobel Prize in Economics; Grangers fundamental principles were that 1) cause happens before effect, and 2) a cause necessarily contains unique information concerning future states of its effect. In details the so-called Granger causality is a specific computation that assumes a linear stochastic process, and as such, it was shown to be entirely equivalent to transfer entropy computed by other means (in information theoretic by the Kullback-Liebler divergence appropriately conditioned) in the special case of a linear stochastic process with Gaussian noise. So said, while the underlying principles of Granger are the same, the details of computation may differ.

Influence can now be described within this formalized framework as related to, but somewhat distinct from leadership, depending on if we are relating interactions between agents in terms of information theory, reduction of uncertainty, or some other underlying principle, including the potential goal of controlling the system. Consider that some agents in a group may be leaders, with various ways to interpret this phrase to be stated subsequently below. A measure of leadership may be associated with information flow for example, or as a proxy for causal influences that leaders may change states, before other agents, a concept which will follow analogously to cause that comes before effect. An influential member of a group is not necessarily a leader, although in some sense influence is a kind of leadership de facto in the sense that influence is comparable to the possibility to cause others to change their behavior (dynamics).

So said then what is the difference between influence, causation, and leadership, from the perspective of information flow? In some interpretations then, influence or causation over others and leadership are almost synonymous but with important distinctions. When leadership is viewed through
the lens of reduction of uncertainty (thus measurable by causation inference and information flow),
then causation and influence becomes a synonym for leadership. Therefore, if a leadership action is
active and observable, then causation and information flow are relevant concepts that enable one to
define and empirically score the leadership. However, there are other notions of leadership that are
clearly beyond the scope of information flow. Herein, by using a taxonomy of leadership, we expand
beyond the typical causation and information flow concepts to allow for those features which
may be missed through the narrow interpretation of entropy, including structure, degree to which
agents are informed, distribution, time and space scales, and target-drive are some of the other
aspects that we will discuss here.

III. PRINCIPLE COMPONENTS OF LEADERSHIP

In this section we offer several mathematical definitions for what we believe are a starting point
for the most basic components of leadership. We begin in Section III A by outlining a general
mathematical framework which we will adopt in Section III C where we outline these components.

A. Framework: Dynamical Systems, Stochastic Processes, and Entropy

To capture various forms of leadership, consider dynamics of individuals (with potential interac-
tions among them via a network) together with dynamics of the group determined by the individuals,
modeled by the general form of ODEs:

\[
\begin{align*}
\dot{x}_i &= f(S_{ij}(t)x_1, \ldots, S_{in}(t)x_n; \mu_i(t); \xi_i(t)), \\
y(t) &= g(x_1(t), \ldots, x_n(t)).
\end{align*}
\]  

(1)

In this general model class, \(x_i(t)\) represents the state of the \(i\)-th individual at time \(t\) \((i = 1, \ldots, n)\),
\(S = [S_{ij}(t)]_{n \times n}\) is the (time-dependent) adjacency matrix (also known as the sociality matrix) of
a network encoding the structure of interactions, where \(S_{ij} \neq 0\) if it is possible for \(j\) to (directly)
impact the state of \(i\). Furthermore, \(\mu_i(t)\) denotes the parameter (vector) associated with \(i\), and
\(\xi_i(t)\) is noise. The function \(f\) models how the dynamics of each individual depends on their own
state and parameter(s), the state of others in the network, and noise. Finally, the state of the
group is determined by the state of the individuals through the function \(g\); for example, taking
\(g(x_1, \ldots, x_n) = \frac{1}{n} \sum_{i=1}^{n} x_i\) defines the group state as the average of the individuals states.

A separate and complementary perspective is to model/represent the individual and group dy-
namics as a multivariate stochastic process, focusing on stationary variables \(X_i(t)\) and \(Y(t)\). From
this perspective, the relationship between the group variable and the variables are encoded in the
conditional distribution function

\[
p(y(t)|x_1(t^-), x_2(t^-), \ldots, x_n(t^-)),
\]  

(2)

where \(t^- = (t-\tau, t)\) denotes time history of the system, taking into account a time lag of \(\tau \in (0, \infty)\).

We point out that there is intimate connection between a dynamical system [such as one defined
by Eq. (1)] and a stochastic process, generally through an underlying (ergodic) measure\(^{33}\), where
the uncertainty associated with the state of the variables is generally related to the distribution
of initial conditions and noise in addition to the coupled dynamics. For a deterministic system,
the randomness initiates exclusively from (experimental) imperfection of choosing and determining
the initial condition, and the evolution of uncertainty can be treated as a stochastic process. Thus entropy methods are naturally associated even with otherwise deterministic dynamical systems Eq. (1) in terms of the associated stochastic process.

From the stochastic representation (2) of the dynamics, we can define an individual’s observed influence on the group using various forms of conditional mutual information. For example, the (unconditioned) mutual information (MI)

$$I(x_i(t^-); y(t))$$

measures the apparent influence of $i$ on the group, aggregated over both direct and indirect factors. On the other hand, after factoring out indirect factors, the “net” influence of $i$ on the group can be measured by the conditional mutual information (CMI)

$$I(x_i(t^-); y(t)|x_{\bar{i}}(t^-)),$$

where $\bar{i} = \{1, \ldots, n\}/\{i\}$.

Note that Eq. (1) itself does not uniquely determine the distribution in Eq. (2), due to the possibly different states/trajectories the system can follow depending on initial conditions, parameters, and other factors; unique ergodicity and fixed parameters are possible assumptions if we wish to discuss uniqueness. Equation (1) can be interpreted as modeling the possible interactions among the individuals, although these interactions may or not not be realized in a particular setting depending on the states the system operates in; on the other hand, the PDF in Eq. (2) encodes (intrinsic) dependence between the group variable and those of the individual variables without necessarily matching the structural information in Eq. (1), even if such dependence comes from dynamics of Eq. (1).

Next, we distinguish between intrinsic states of the system versus observed states, as a key aspect in mathematical interpretation of any process, including group roles of leadership, is the concept of measurement of observables, from the underlying process. In fact, the concept of leadership, and information flow, can be dramatically obscured depending on the details of the observables (extrinsic variables) relative to the underlying system (intrinsic variables). We use $\hat{x}_i(t)$ to represent the observed state regarding $x_i(t)$, and similarly, $\hat{y}(t)$ for the observed state regarding $y(t)$. We represent the observations over a finite time window, producing observational data

$$\{\hat{x}_i(t); \hat{y}(t)\}_{t \in I}.$$ 

B. Reference Frame of Group Dynamics, Time Scale, and Leadership

Proper characterization and interpretation of leadership requires the (subjective) identification of a reference frame. We argue that defining such a frame needs to include making at least the following three choices:

1. Variables (position, velocity, acceleration, direction of motion, some combination of these, or else.) Depending on the choice of variables, different types of leadership can emerge and be identified.

2. Temporal resolution and time lag. What is the temporal resolution of activities that is of interest? Seconds, days, or years? Then there is the issue/point about time lag. How far in the past is an action thought to have potential impact? If the time lag is too large, potentially any individual can have some level of influence and therefore be a candidate for leadership;
on the other hand, too small of a time lag might prevent detection of the (time-delayed) dynamics of the group in response to an individual’s actions.

3. Definition of a group and what it represents. For example, a group can contain everyone within a spatial domain, or can be based on age, gender, etc.

C. The Components

In broad terms, we define a leader to be any agent in a group that has an asymmetric potential to impact the trajectory of agents in the group. As we explore below, the source of this asymmetric impact or influence may be due to group structure, individual information or emerge from social interaction rules alone. Further, the distribution and time and length scales of the resulting leadership may vary considerably. In this section we construct a series of informative classifications which we will refer to as the components of leadership.

Structural Leadership. Structural leadership encompasses a wide range of leadership which fundamentally relies on the structure of the animal society such as an individuals rank, social norms, dominance or social hierarchy. In this discussion we use the sociality matrix defined in Eq. 1 to encode these norms, ranks and hierarchies into the model. In particular, consider the directed graph associated with the sociality matrix $S$ where there is a directed edge $i \to j$ if and only if $S_{ij} \neq 0$, we define node $\ell$ in to be a a structural leader of a group of nodes $\mathcal{F}$ (not including $\ell$ itself) if, for every element $j$ of $\mathcal{F}$, there is a directed path from $\ell$ to $j$ in $\mathcal{S}$. In other words, $\ell$ is a structural leader of $\mathcal{F}$ if the set $\mathcal{F}$ is a subset of the reachability set of $\ell$ in the graph. For a given group $\mathcal{F}$ (typically taken as the set of all nodes), we call the set of all such structural leaders $\mathcal{L}$.

In our caribou example from the introduction, we might expect to find strong hierarchical relationships between males during the rut, leading to structural leadership. More generally, individuals being influenced differently by others according to their gender, age or reproductive status, could naturally be encoded by a sociality matrix and therefore classified as structural leadership.

Structural leadership is, mathematically, a very weak definition of leadership as it really only takes into account the capacity for an individual to be a leader. In some ways this component should really be seen as a minimal condition for leadership to occur within a mobile animal group. In reality however this form of leadership is quite important because it encodes the social norms, ranks and hierarchies of the society.

Informed Leadership. Informed leadership arises when a subset of the group are differentially informed and motivated to act on that information, e.g., a subset of the group senses a resource or has information about a migration route. Such leaders may be anonymous, or may indicate that they have information, for example by changing speed or signaling.

In the case of our migrating caribou, both the experienced individuals leading the long-scale migration movement, and the individuals responding to local food and predation cues provide complementary examples of informed leadership.

The concept of informed leadership is intuitively sensible but mathematically it is both difficult to define and perhaps impossible to accurately infer.

Emergent Leadership.

Asymmetrical influence, and thus leadership, may arise from social interactions rules alone, in the absence of social structure or differential information; we term this emergent leadership. This would be the case if animals used anisotropic social interaction rules. For example when individuals...
are more influenced by other individuals that are in front of them, and individuals in more frontal
positions of the group are more influential, even if they have no additional information, motivation
or status. Such emergent leadership has recently been shown to be the case in our migratory caribou
example.30

Alternatively, if individuals are more influenced by faster-moving group-mates55, then those faster-
moving individuals will have more influence. If those individuals are moving more quickly in
response to information, or to signal dominance, then this would be informational or structural
leadership, respectively, but if the increased speed is purely a function of the group dynamics, this
would be an example of emergent leadership.

We note that an external observer may not be able to reliably distinguish between structural,
emergent and emergent leadership from the trajectories of the agents alone. This is an important
distinction. Some animals lead as a result of social rank and hierarchy56,57, others lead because
they have additional information or motivation58–61, and in other scenarios animals may
lead via asymmetries in social interaction rules30. Conventional/often-used leadership inference
methods however such as positional, causal inference, information flow etc. cannot necessarily tell
the difference between these three different axes of leadership.

**Distribution of Leadership.** In animal groups decisions range from full distributed among all
group members (‘democratic’) to dominated by a single or a few individuals (‘despotic’)8,12. It can
be informative to quantify the number of individuals involved in a leadership role within the group.
Similar to12 we refer to this as the distribution of leadership which we define on a continuum that
lies between centralized and distributed leadership. Let \( \mathcal{L} \) be a set of structural leaders defined
using any component of leadership. If the cardinality of \( \mathcal{L} \) is \( O(1) \) then we say that the elements
of \( \mathcal{L} \) are centralized leaders. If instead the cardinality is \( O(N) \), where \( N \) is the number of agents in
the group, then we say that the members of \( \mathcal{L} \) are distributed leaders.

At the scale of the entire herd, we might expect our migrating caribou to fall somewhere on
this spectrum, bookended by primate societies with an alpha individual on one end and leaderless
fission-fusion fish schools on the other. If we consider the mother-calf pairs as subgroups, we would
expect the mother to be a centralized leader. However, in a larger group containing many such
pairs, we would expect distributed leadership shared between the mothers.

**Temporal Scale of Leadership.**
A leader may not be actively influencing the motion of other agents at all times and it is thus
useful to quantify and understand the time scales for which a leader qualifies as a leader under
any of the components of leadership. Here, we consider two notions of time scales—consistency
and granularity. For the following discussion consider dynamics of individuals, represented by
discrete-time observations \( \{x_i(t)\}_{t=0}^T \).

**Consistency** of leadership is simply defined as the proportion of the observation window for which
a leader qualifies as a leader. More specifically, we classify leaders as persistent over the observation
window if it is identified as a leader for the entire time window. Conversely, we classify a leader as
ephemeral if it only qualifies as a leader for some small time window \([t, t + \tau]\), with \( \tau \ll T \). A similar
temporal leadership scale is presented in12 which ranges from variable to consistent but attempts
to capture the same notion.

The **granularity** of leadership concerns the resolution of time steps for which an individual acts as
a leader. For example, a leader for daily activities might be different from one that is for seasonal
activities. We can check for granularity by altering the time step we examine the dynamics under.
In particular, quantify leadership using only the observations \( \{x_i(kt)\}_{t=0}^{T/k} \) \((k > 1)\) for a large range
of \( k \). If a leader only acts on a coarse basis then they may not register as a leader for small \( k \) but
may then register as a leader for some larger \( k \). In contrast a fine-scaled leader may register for
In our migrating caribou example, the experienced individuals leading the broad migration path exhibit leadership that is persistent, but perhaps has coarse granularity. In contrast, the leadership of those animals responding to resources or predation threats along the way is ephemeral and has fine granularity.

Time scales present several challenges when attempting to infer leadership roles from a time series. If the granularity or observation window length do not match the natural time-scales of leadership then leadership events may be completely missed or misclassified. For example, consider a structural leader $\ell$ with the property that $I(x_i(t^-); y(t)|x_i(t^-)) = 0$, i.e., a structural leader that does not directly influence the group—although it has the potential to. Regardless of the inference method such a potential leader will always be misclassified. Similarly consider an informational leader that only leads when they are within some radius to a known resource. Say that this event only occurred for a very short time window $[t, t+\tau]$, with $\tau \ll T$. If you only consider leaders that lead for the entire observation window, most aggregate measures will wash out such an ephemeral leadership event. For these reasons, carefully considering both consistency by studying sub samples of the data set as well as granularity by down sampling the data and retesting one will be able to obtain a much clearer picture of the leaders that are present in a mobile animal group.

Reach of Leadership. The reach of a leader determines the spatial, or more generally, topological scale for which an agent qualifies as a leader. This spatial scale may be metric (lead everyone in a ten-meter range), or topological (lead all individuals up to two neighbors away in the sociality matrix). Reach naturally lies on a continuum between local and global. If an agent exemplifies some form of leadership over all individuals this would be global reach; if an individual only leads some small subset of the group then this leader is considered local. To quantify reach one simply computes the spatial scale (either metric or topological) for which an agent holds a leadership role. We define reach to be the maximum radius away from an individual for which they have the capacity to lead other individuals. This may be a distance in space or the maximum shortest path to a follower on the sociality graph.

In the case of our migrating caribou, the experienced migrants leading the entire herd on its broad migration path, would have global reach, while the mother leading her calf on a finer-scale would have local reach.

Target-Driven Leadership A target-driven leader uses a series of deliberate control inputs such as calls, explicit motions, etc. to guide a group toward a particular target state or set of target states.

To be more precise, we characterize a target-driven leader as an individual that not only influences the group, but deliberately controls the group toward some target state. In addition, the removal of such an individual should result in the group not going towards the target state. Mathematically, we define this component as follows. Given that $\mathcal{A}$ is a set of target states, then an individual is a target-driven leader if both of the following hold:

$$I(x_i(t^-); y(t)|x_i(t^-)) > 0$$  \hspace{1cm} (6)

and

$$y(t) \rightarrow \mathcal{A} \text{ as } t \rightarrow \infty.$$  \hspace{1cm} (7)

That is, the individual directly influences the group as a whole and that influence results in the group tending toward the target states in the limit.
An example of a target-driven leader is a sheep dog. These dogs run behind a group of sheep and through an intentional series of signals such as barking, eye contact and body posture the dog deliberately controls the sheep herd toward a given target state such as a barn or field.

**Observability of Leadership.** When we observe an animal society we do so imperfectly, mainly in two ways. First, any observed quantity is subject to noise and measurement errors. Secondly, and perhaps more importantly, there may be elements of the society which go *unobserved*. Such hidden variables and states may in turn act in our interpretation of leadership. In fact, the strongest leadership might not be detectable if the data are not appropriate. Across various taxa, leaders may use vocal cues, gestures or movements that are too fine to be picked up by GPS (e.g. pre-flight flapping) to initiate or control movement. If the resulting movement is synchronized, leadership inference based on trajectories will fail. Worse, if in the resulting movement, the least dominate individuals respond first to the cues, it could appear as though those individuals are leading.

In the case of our migrating caribou, lead animals may stand up to signal departure, or motivate others to start moving. This would not be captured by GPS tags and so would be *hidden* to inference methods based on trajectories alone.

Quantification of hidden leadership in practice is quite difficult by definition. Namely, if you have detected leadership it was observed. Doing this in theory however is quite trivial. As defined in Section III A we define the full system dynamics via $x$, $y$, $S$ (and/or some mix of these). When the system is being observed, the observed variables, denoted $\hat{x}$, $\hat{y}$, and $\hat{S}$, can differ from the true ones. We term an individual a hidden leader if it is a leader defined in terms of the intrinsic variables $(x, y, S)$ but no longer a leader defined for the observed variables $(\hat{x}, \hat{y}, \hat{S})$; a leader that is not hidden is then called an observable leader.

### IV. CASE STUDIES

As an important step toward illustrating the taxonomy of leadership outlined in the previous section is useful we explore the anatomy of leadership for a well-known model system in which a lot of the “answers” are known, or at least widely accepted. This will give us an interpretation-free environment to explore this state space. Of course, just exploring such a toy model is insufficient and empirical data should at least be considered. This situation however is much messier as many leadership rules in actual mobile animal groups remain unclassified and many studies must rely on trained individuals. We hope that this anatomy of leadership helps practitioners begin to dissect the leadership roles in a broader class of empirical data.

#### A. ‘Zonal’ Flocking/Schooling Model

In this model groups are composed of $N$ agents. First we state the technical details of the underlying dynamics. Following that, the leadership roles will be described within the context and language of this paper.

For each agent, numbered $j = 1, ..., N$, and each time $t$, a position vector $c_j(t)$ and a velocity vector $v_j(t)$ are maintained. At each time step agent $j$ computes a desired direction $d_j(t)$ based on neighbors in three different zones, depicted in Figure 1.

The first zone to consider is called the *repulsion* zone and is denoted by $R$. This zone ensures that personal space is maintained for each agent. If any other agent is in the repulsion zone $R$, for
focal individual \( j \), then the desired direction in the next time step is defined by

\[
d_i(t + \Delta t) = - \sum_{j \neq i, j \notin R} \frac{c_j(t) - c_i(t)}{|c_j(t) - c_i(t)|}.
\] (8)

This desired direction ensures that a collision will not occur at time \( t + \Delta t \). However, if for the focal individual \( R = \emptyset \) then the focal individual attempts to get closer to agents in their attraction zone \( A \) and orient with agents in their orientation zone \( O \). This is accomplished by choosing a desired direction at time \( t + \Delta t \) in the following way:

\[
d_i(t + \Delta t) = \alpha \sum_{j \neq i, j \in A} \frac{c_j(t) - c_i(t)}{|c_j(t) - c_i(t)|} + (1 - \alpha) \sum_{j \neq i, j \in O} \frac{v_j(t)}{|v_j(t)|}.
\] (9)

Where \( \alpha \) is a parameter that controls the relative strength of attraction and alignment. Consider for example a flock of geese which would have a relatively low \( \alpha \), but a swarm of insects on the other hand would have a relatively high \( \alpha \). In this manuscript we choose \( \alpha = 0.25 \) which puts more weight on heading than position.

After the desired direction is assigned, the position at \( t + \Delta t \) can be computed by

\[
c_i(t + \Delta t) = c_i(t) + d_i(t + \Delta t) + \xi.
\] (10)

Where, \( \xi \in \mathcal{N}(0, \beta) \), adding a small amount of noise to each heading.
In the context of leadership inference it is helpful to make two modifications to this simple model (1) give each agent a social circle and (2) add “informed” individuals to the group.

**Explicit Social Interactions** To add explicit social interactions we introduce a sociality matrix \( S = [S_{ij}(t)]_{N \times N} \). \( S_{ij} \neq 0 \) if agent \( i \) can interact with (be influenced by) agent \( j \) and 0 otherwise. To take this into account the desired-direction computation is modified to only reflect individuals in the agents social circle (rather than anyone in \( A \) and \( O \), i.e.,

\[
d_i(t + \Delta t) = \alpha \sum_{j \neq i : j \in A} S_{ij} \frac{c_j(t) - c_i(t)}{|c_j(t) - c_i(t)|} + (1 - \alpha) \sum_{j \neq i : j \in O} S_{ij} \frac{v_j(t)}{|v_j(t)|}.
\]

(11)

The sociality is useful for hypothesis testing, it allows interaction rules to be explicitly built in. This is an advantage as you can then see if post-facto the interaction rules placed in the model can be extracted by the inference method.

**Informed Group Members** To simulate “informed” group members, a subset of the agents are given knowledge of a preferred direction \( g \) (more generally each informed agent is given their own not necessarily equal preferred direction \( g_i \)). This preferred direction may be part of a migration route or the direction of a prey or known resource. Non-informed group members, have no knowledge of \( g \) and may or may not know which individuals are informed. To integrate this into the model the informed individuals balance between the social interactions and their preferred direction with a weighting term \( \omega \). In particular,

\[
\hat{d}_i(t + \Delta t) = d_i(t + \Delta t) + \omega g_i.
\]

(12)

If \( \omega = 0 \) the preferred direction is completely ignored and only social interactions are followed. As \( \omega \) increases toward 1 the influence of the preferred direction is balanced with influence of the social interactions. With \( \omega > 1 \) the preferred direction is favored over social interactions.

**B. Conceptual Examples**

The following examples are each chosen to highlight aspects of the taxonomy associated with the anatomy of leadership terms defined above, to illustrate their meaning, and emphasize the concepts. By using our language in the context of these flocking and swarming models, hopefully the power of the terminology will be emphasized, and the utility of our development of a universal language will become clear. In the following section, we will present several natural real world examples of animal interactions, and then describe the aspects of their behaviors also within the language of this anatomy as developed here.

We first consider a mobile-animal group where each member is governed by Eq. 10, with \( \alpha \in [0, 1] \) i.e., a group of random walkers that follow social interaction rules characterized by attraction, repulsion and orientation. Notice that this is identical to having explicit social interactions with an all-to-all adjacency matrix.

This is an interesting case because under a colloquial understanding of “leadership” there is no leader in this group. In particular, each member of the group has the capacity to influence every
other member but they only do so through indirect social interactions (viz., attraction, orientation and repulsion). In this simulation we know each agent lacks a preferred direction or any kind of specialized information and no social hierarchy exists. With this domain knowledge the incidental social interactions, such as those caused by repulsion, cause a real problem for most influence/causal inference algorithms. For example, if one blindly applies optimal causation entropy\textsuperscript{26} to this system to infer who influences whom then you receive an all-to-all influence graph (seen in Figure 2). Without domain knowledge it would be tempting to conclude that each member actively influences each other member but in reality the information flow is completely incidental and a result of the repulsion component of the social interaction rules.

Figure 2. Optimal Causation Entropy output for two different leadership models. Blue edges imply information flow between each node (agents).

We can gain more insight into this scenario by using the taxonomy constructed in this manuscript. In particular, this setup results in fully-distributed persistent uninformed target-less global structural leadership. Each agent has a nonempty reachability set, so the set of structural leaders is every node. This implies distributed leadership as there are exactly \(N\) structural leaders. Each structural leader has a reach of the entire group, which implies that all leaders are global. These dynamics are autonomous so any leadership seen would occur over the entire observation window and at all granularities. Thus each leader is persistent. There is no target state and no group member is actively driving the group toward any particular goal so there are no target-driven leaders. The entire system is being observed and so there are no hidden leaders. With this more well-rounded analysis of this system we now have more insight into the nature of information flow that occurs in this system and could better utilize the results presented in Figure 2. However, what if the dynamics changed and some individuals were informed or targeted?

Now consider a slightly different scenario, where the dynamics are governed by Equation 11 for \(t \in [0, t^*]\) and are governed by Equation 12 for \(t \in [t^*, T]\), where \(t^*\) is fairly close to \(T\). At time \(t^*\) a stationary member (labeled \(h\)) who lies outside of the attraction, orientation and repulsion zone of the group vocally calls to the group to inform them of a resource and \(m < N\) agents hear this call. Individual \(h\) then continues to call to the group at regular time intervals \(\tau\) while remaining stationary. These \(m\) agents then begin to act on this information, utilizing this new preferred direction according to Equation 12 with \(\omega = 1\).
The diversity of leadership in this simple example is quite interesting but would be lost on the
majority of inference algorithms. For example, if one were to apply optimal causation entropy \( t \) to
these trajectories. You would receive an identical result to the results depicted in Figure 2 however
a single node, agent \( h \) in particular, would have no links in or out of it. Similar to optimal causation
entropy most causal inference algorithms applied to trajectories would come to a similar conclusion
about this scenario—completely missing the intricate leadership dynamics.

If instead of applying a causal inference algorithm to these trajectories we use the anatomy of
leadership we can begin to pull apart the intricate leadership dynamics that are present. Similar to
the previous example, for \( t \in [0, T] \) this group exhibits fully-distributed persistent global structural
leadership for the same reasons outlined above. However, the story changes for \( t \in (t^*, T] \). First of
all, we now have a hidden target-driven leader. Namely, node \( h \). Agent \( h \) is leading the group to a
target state through auditory cues and remains stationary. This means that any trajectory based
observation of this system would fail to infer this hidden leadership role. The reach of \( h \) is only
the \( m \) agents that heard the call not the entire group and \( h \) is an ephemeral leader as they only
lead for \( t \in [t^*, T] \) and at a granularity of \( \tau \). The \( m \) agents that hear and react to this call become
ephemeral informational leaders for \( t > t^* \).

C. Discussion of Real World Animal Behavior: A Rabbi, A Priest and A Beaver Walk Into a Bar...

In parallel to the previous section highlighting our anatomy terms in the setting of mathematical
models, and their configurations, here we discuss real world animal interactions, and we do so in a
manner to emphasize the terminology of our anatomy of leadership taxonomy.

We expect to find structural leadership in relatively stable animal groups, often having complex
social hierarchies, such as cetaceans, wolves, wild dogs, elephants and primates\(^{15,57,68–70} \). The
canonical example is the so-called ‘alpha’ individual in a primate society, who has some level of
control over an entire group over a long period of time (assuming he society is stable)\(^{71} \). In our
taxonomy, this dominant individual would be a persistent, centralized, structural leader with a large
reach. It is important to note that in such societies, structural leadership may be well correlated
with informational leadership. For example, a matriarch elephant may have better information
about rarely visited water holes, as well as greater per-capita influence to lead her group to them.

We expect informational leadership to dominate in animal groups composed of unrelated individ-
uals and unstable membership (i.e., fission-fusion dynamics), such as fish schools and bird flocks. A
single arbitrary member of a fish school may perceive a respond to a threat, causing those around
it to also startle, or the entire group to make an evasive maneuver\(^{60} \). This is an example of centralized,
ephemeral, informational leadership with a limited or global reach, depending how much of the
group responded. Similarly, some fraction of the same school might have information about where
or when a food resource might occur and lead the entire school to that time-space location\(^{50,51,59} \).
In our terms those fish are distributed, ephemeral, informational leaders with global reach.

Informational leadership is also common for movement at long length scales. In flocks of pigeons,
better informed individuals act as leaders during homing flights\(^{60} \). (However, it should be noted
that pigeons also exhibit a structural hierarchy too\(^{19} \).) During migratory movements, older, more
experienced, birds guide groups on efficient migration routes\(^{5,52} \). In both of these examples the
informed birds are centralized, persistent, target-driven, informational leaders with global reach.

In migrating white storks some individuals actively seek thermals updrafts, which are neces-
sary for them to get efficient lift to complete the migration, while others tend to copy, by moving
towards individuals who are already in thermals\(^{72} \). This is a specific example of a general phe-
nomenon, emergent sensing\(^{3} \), in which a group spans an environmental gradient and individuals in
the ‘preferred’ end of the gradient alter their behaviour (purposefully or not) in a way that cause
the entire group to climb the gradient\textsuperscript{54,73}. In general such leadership would be distributed and
ephemeral (although could be persistent if, like in the storks, the same individuals always find the
thermals) informational leadership with global reach.

V. AFTERWARD

Traditional approaches to leadership inference have focused on a single defining characteristic,
e.g., position within a group, social hierarchy, information flow or influence. We believe that, in
general, none of these concepts alone fully captures leadership. In this manuscript we have begun to
show that a multifaceted approach where multiple axes of leadership are analyzed provides a more
complete classification of the leadership structure. This formalism should serve to link questions
about empirical systems with the appropriate analytical tools to address those questions. While
this taxonomy we provided is surely not complete we hope that this effort will serve as a starting
point for formalizing a multifaceted approach to leadership inference.

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