The dynamics of dominance: open questions, challenges, and solutions

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**Abstract**

Although social hierarchies are widely recognized as dynamic systems, they have historically been treated as static entities for practical reasons. Here, we ask what can we learn from a dynamical view of dominance that we can’t learn from a static perspective, and provide an agenda for exploring the dynamics of dominance hierarchies over the next decades. We identify five broad questions regarding the dynamics of dominance at the individual, dyadic, and group levels. Although challenges remain for answering these questions, we propose avenues for overcoming them. We identify some conceptual areas that currently lack clarity in the literature and suggest refinement of dominance dynamics concepts to overcome these issues. We show that further methodological advances are needed to reliably infer dynamics at the group and individual level. At the dyadic level, we suggest theoretical model development paired with tests in captive systems as the most promising way forward. Across scales, model systems where rank can be manipulated will be extremely useful for targeted testing of hypotheses about the dynamics of dominance hierarchies. Long-term individual-based studies will also be critical for understanding the impact of rare events, and for interrogating dynamics that unfold over lifetimes and generations.

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|  | **Open questions** | **Challenges** | **Solutions** |
| **Individual Level** | How and why do individuals change position in the dominance hierarchy? | Lack of conceptual clarity about rank dynamics at individual level | Multiple social mobility concepts presented here |
| Accurately measuring social mobility | Account for uncertainty in rank measurement when identifying changes |
| Determine appropriate time-scale at which to assess social mobility |
| How do dominance trajectories across life produce fitness trajectories and impact selection on status-seeking behaviour? | It is difficult to study processes occurring at lifetime scale | Long-term individual-based studies |
| Theoretical models integrating behaviour and dominance trajectories |
|  |  |  |  |
| **Dyadic level** | When & why do dyads engage in contests? | Requires data that go beyond direct interactions--e.g., initiation, avoidance, long-distance signals, behavioural state, etc. | Develop methods for studying the lack of interactions |
| Account for opportunity to interact |
| Distinguish the roles of dominant and subordinate individuals in driving interaction rates |
| How do dominance relationships form and dissolve? | Requires high-resolution interaction data | Captive systems with the capacity for high-resolution data collection (e.g., automated tracking) |
| Lack of theoretical framework to guide empirical studies | Development and testing of interaction-to-relationship models |
|  |  |  |  |
| **Group level** | What are the causes and consequences of social instability? | Lack of conceptual clarity about social instability | Social instability concepts presented here |
| Accurately measuring instability | Research into appropriate time-scale at which to measure instability |
| Account for uncertainty in rank measurement when identifying hierarchical instability |
| Rare but extreme instability can have high impact but be difficult to study | Long-term studies that capture naturally occurring extreme instability |
| Experimental manipulation of social instability |

**Table 1.** A research agenda for the dynamics of dominance.

**Introduction**

Dominance is one of the most studied social behaviours, but is typically studied using a static approach in which agonistic interactions are tabulated and used to infer individual ‘rank’ in the dominance hierarchy [1]. These dominance ranks are then compared with other covariates of interest to understand causes and consequences of position in the dominance hierarchy in social systems [2]. Although the traditional static approach has produced valuable insight into the role of dominance in social systems, it side-steps challenges associated with the dynamics of dominance. As a result, many gaps remain in our understanding of how and why dominance hierarchies change over time and what impacts these changes have for of animal societies. Here we highlight these gaps, discuss the challenges to addressing them, and suggest solutions to these problems and promising avenues for future research (Table 1). Specifically, we examine research questions about dynamics of dominance occurring at three scales -- individuals, dyads, and groups (Figure 1). Targeting these gaps in future research will provide an integrative understanding of how dominance operates dynamically to structure societies at multiple scales.



**Figure 1.** Dominance hierarchies are inferred from observed agonistic interactions (A). Dynamics within these hierarchies occur at three scales: (B) individuals change position in the hierarchy, (C) dyadic dominance relationships change over time, and (D) groups experience instability.

**Individual level**

*How and why do individuals change position in the dominance hierarchy?*

Social rank has important consequences for individuals, impacting stress physiology, social relationships, longevity, immune function, and reproductive success [3–5]. For most species, it is unclear what causes individuals to change position in the dominance hierarchy, or conversely, how dominants may preserve their status [6,7]. It is important to understand the causes and consequences of rank changes, both to understand potential selection on status-seeking behaviour [8–10], and because rank changes can shed light on the forces involved in determining social rank in the first place [11]. However, progress in understanding the dynamics of dominance hierarchies is hampered by lack of a clearly defined concept of ‘rank change’. The literature is plagued with redundant and ambiguous terminology such as rank change [12,13], rank reversal [14,15], revolutionary coalition [16], dominance turnover [17,18], social mobility [19–21], and power trajectories [22]. The proliferation of related terms reflects the complexity of the concept--i.e., that position in the dominance hierarchy can change in multiple ways. Thus, there is a need for multiple rank-change concepts and clear distinctions between them.

We borrow concepts from the study of social mobility in humans to delineate categories of how rank changes can occur. Social mobility can occur within generations -- *intragenerational mobility* -- or between generations -- *intergenerational mobility* [23]. Intergenerational mobility measures the extent to which parental dominance rank predicts offspring dominance, whereas intragenerational mobility describes movements of individuals in the hierarchy over their lifetimes. Patterns of intergenerational mobility are an ongoing focus of research in economics [24–26]. However, intergenerational mobility is comparatively underexplored in non-human animals, with the important exceptions of work on rank inheritance and maternal effects on dominance in some systems [27,28]. There are two types of inter- and intragenerational mobility that arise via different processes [29]: *active mobility*, which involves a reversal of a previously held rank relationship and *passive mobility*, which is a change in rank that occurs without any reordering of the hierarchy. Passive mobility results from demographic processes like births/deaths and immigration/emigration -- for example, if the highest-ranked individual dies and no active intragenerational mobility occurs, the second-ranked individual improves one position through passive intragenerational mobility [30,31]. Active mobility can result from multiple processes such as winner/loser effects, changes in rank-associated covariates, or feedbacks between multiple influences on rank [32,33]. In future research, distinguishing among these different types of social mobility will help to bring conceptual clarity to research into hierarchy dynamics and will reveal diverse drivers and impacts of mobility.

Methodological groundwork exists for inferring patterns of social mobility, but more work in this area is needed. Mobility can be measured in absolute units (e.g., increase/decrease in number of individuals dominated) or relative to other members of society (e.g., increase/decrease in rank standardized for group size) [34,35]. Contrasts in the causes and consequences of relative and absolute mobility can reflect biological differences in the ways animals compete [36]. Many methods exist for inferring a rank order from a sample of animal contests [37,38], and numerous studies have evaluated the efficacy of these methods at finding rank orders [38–40], but very little work has evaluated the efficacy of these methods for inferring changes in rank over time. Consequently, applying these existing methods to the study of social mobility will require some refinements. First, if social mobility is rare, then noise in calculations of social rank will make it difficult to distinguish true mobility events from false identification of rank changes [29]. Thus, the study of social mobility requires the development of approaches that accurately estimate social mobility and account for uncertainty (Box 1). Additionally, more work should focus on measuring intergenerational mobility. To measure intergenerational mobility, researchers can use parent-offspring correlations between rank, as is often done in economics. An alternative approach is to compare observed offspring rank to a rank based on a reference model where offspring win and lose interactions with equal probability as their parents [41]; this approach may be less biased by differences between parents and offspring in observation time or interaction rate. Finally, more work needs to address how to decompose mobility into active and passive components. Techniques have been advanced for decomposing changes in ordinal rank (e.g., rank 1, 2…n) into passive and active mobility [29], but this method does not work for cardinal ratings (e.g., David’s scores, Elo-rating), which are sometimes preferable (e.g., when measuring hierarchy steepness; [42–44]). In sum, a fruitful path forward is to continue refining methods for inferring hierarchy dynamics at the individual level.

Box 1 - Methodological challenges in inferring hierarchy dynamics

A few studies have made progress towards improving the efficacy of ranking methods for identifying mobility, but considerable work remains. Approaches that determine ranks based on discrete subsets of the data and infer changes by comparing these rank orders overestimate the true amount of mobility [29]. This issue can be alleviated by using an “updating” process to rank individuals in each study period based on prior ranks informed by newly collected data. This updating approach is implemented by defualt in the Elo-rating and Glicko-rating methods [43,45–48], but can also be incorporated into other commonly used types of ranking methods such as David’s Scores or matrix reordering [29].

A crucial methodological decision when identifying social mobility is to determine the time period over which potential dynamics are assessed. The more frequently potential changes are assessed, the more potential changes can be found. For instance, assessing an individual’s change monthly over a year can lead to the identification of 11 changes in position, whereas measuring mobility daily over the same period could potentially identify 364. Accordingly, sampling for dynamics more frequently leads to the identification of more changes [29]. There are dangers to assessing potential changes both too frequently or too infrequently -- if changes are assessed too rarely, real changes can be missed or misinterpreted [43], while assessing changes too frequently can lead to inference that is overly sensitive to uncertainty in an animal’s relationships. If only a few individuals or interactions are sampled during the periods over which mobility is assessed, this will lead to an overestimation of the number of changes and an underestimation of the rate of change (i.e., rank instability; see Group level section). Data-splitting approaches can be used to assess the timescale over which a rank order is predictive of future interaction outcomes [49], providing a guide for the appropriate time-scale over which to assess potential hierarchy dynamics. Finally, the time-scale at which rank effects occur in the study species should be incorporated into decision-making about the time-scale over which hierarchy dynamics are assessed. For instance, inferring daily dynamics will be misleading if rank effects only manifest over longer time-scales or if many dyads don’t interact daily.

The last challenge for measuring social mobility is identifying and accounting for uncertainty. There is a pressing need to expand methods for detecting social mobility to account for uncertainties in rank orders. Otherwise, measurement error can lead to the overestimation of social mobility and lead the noise of spurious social mobility to swamp the signal of true social mobility. This is particularly challenging because it is difficult to distinguish *measurement uncertainty* in rank order -- arising from sampling bias, observer error, and missing data -- from *biological uncertainty* in rank relationships among individuals (McCowan contribution to this issue). In fact, because active intragenerational mobility by definition involves changing dominance relationships, biological uncertainty in rank orders during mobility is expected to increase during periods of active mobility. Therefore, a crucial step is to develop methods for measuring and interpreting uncertainty in estimates of social mobility. Some studies have introduced methods for quantifying uncertainty around inferred dominance ranks or scores [39,46,50], but no study has yet used these uncertainty estimates when inferring hierarchy dynamics.

*How do dominance trajectories across life produce fitness trajectories and impact selection on status-seeking behaviour?*

Dominance rank is often linked to fitness, but we know relatively little about the temporal dynamics of these effects. Effects of rank could be ephemeral, with each instance of rank change causing corresponding changes in rank-related outcomes ([31]; Tung this issue), or they could be persistent and manifest even after individuals undergo social mobility [51]. Moreover, the way in which individuals move through the hierarchy over the course of their lifetime can moderate short-term influences between rank and fitness [7,52]. For instance, the costs of dominance status acquisition can offset the benefits of high rank [53–55], making it necessary for individuals to hold high status for sufficient time to gain a net benefit. Furthermore, individuals could all show similar trajectories over life -- in such a case, subordinates may appear to be paying a fitness cost by being subordinate, when instead they will eventually enjoy dominant status, and in fact all individuals may experience relatively equal lifetime fitness. The dynamics of rank across development and life-history stages (e.g., dispersal [56]) add further complexity to the ways that dynamic rank link to fitness.

Critically, in addition to modulating short-term associations between rank and fitness, dominance trajectories can reflect selection on status-seeking behaviour or influence the stability of social systems. For instance, some have suggested that an on-average tendency to improve in social status over the life course is critical for maintaining persistent groups [35]. Theoretical work suggests that if subordinates can achieve high status by queuing, this relaxes selection on status-seeking behaviour and could lead subordinates to be more tolerant of despotism by dominants [52]. Subordinate individuals with similar rank may vary in status-seeking behaviours (e.g., information collecting, prospecting, challenging dominants) that later influence their trajectory in social status [57–59]. In sum, to truly understand the influence of rank on fitness and the evolution of status-seeking behaviour, it is necessary to examine dominance trajectories over individuals’ lifetime to understand how fitness outcomes vary as a function of rank and mobility over the life course. Here, theoretical models of optimal strategies under different dominance trajectory regimes [52] and long-term individual-based studies will be particularly valuable.

This life-course approach of dominance trajectories also opens an opportunity to take a life-history view of status-seeking behaviour. From this perspective, how individuals invest in status-seeking behaviour across a lifetime will depend on a combination of the fitness consequences of status, the longevity of such effects, and the probable mechanisms of rank change (i.e., intra- vs. intergeneration mobility, active vs. passive mobility) [52,58]. For example, in systems where rank and fitness are highly correlated, and upward social mobility is largely passive, selection may favor life-history strategies that increase longevity to maximize the chances of attaining high rank by persisting in the queue. Conversely, in systems where active mobility predominates, selection may favor early investment in growth in order to maximize the probability of displacing dominants. Such integration of social dynamics and life-history theory will contribute to an emerging perspective on life history of social behaviour [60–62]. In total, viewing dominance rank as a trajectory that unfolds over the life course will reveal normative patterns of dominance trajectories, potential alternative strategies to maximizing fitness in hierarchical societies, and the role of social mobility in the evolution of status-seeking behaviour.

**Dyadic level**

*How do dominance relationships form and dissolve?*

A century ago, Thorleif Schjelderup-Ebbe [1] presented a simplistic verbal model of how dominance relationships form and change, stating of a contest between hens A and B: "If B wins she will become the despot, possibly forever but in any case for the time being." Despite a century of research on dominance, very little progress has been made beyond Schjelderup-Ebbe’s intuitions about how interactions impact dominance relationships. When two individuals interact, the status of their dominance relationship is probed, reinforced, or altered [63]. For new relationships, repeated interactions quickly lead to the establishment of a dominance relationship, which is characterized by an overall reduction in aggression [64]. In established relationships, additional interactions typically reinforce the existing dominance relationship, but can sometimes counter it and lead to its reversal. Although dominance relationships are well-understood as a structure resulting from the combination of interactions [63], very little progress has been made towards developing and testing quantitative models of how these relationships arise from their component interactions.

Uncovering how dominance relationships form and dissolve requires the development of *interaction-to-relationship* models of how interactions are integrated to form relationships [65]. These models should be able to reproduce typical patterns of dominance relationships, where established relationships form, remain stable, but can also change to a new stable state after new interactions -- that is, relationships that once formed remain stable “possibly forever, but in any case for the time being.” Feedback loops between interaction outcomes and the drivers of dominance relationships suggest mechanisms by which stable dominance relationships might be pushed over a tipping point [33,66]. Interaction-to-relationship models need to consider a) potential time and intensity dependency in the influence of interactions on relationship status, b) the opportunity for other attributes of individuals or their relationships to influence dominance, and, most importantly, c) underlying cognitive models by which individuals understand their relation to their groupmates.

Empirical studies point to some alternative plausible cognitive models underlying dominance relationships. Individuals may track group consensus about position in the dominance hierarchy [67], track the aggression received by group members and use it to infer position in the hierarchy [68], monitor aggression network structure using transitive inference [68], remember their specific relationship with other members of the group [69], attend to signals reflecting competitive ability [70], or some combination of these models. These models make predictions about how dominance relationships might change under different perterbuations, such as the removal of the dominant individual, changes in physical condition, social mobility among other group-members, or stochastic outcomes of interactions that don’t align with the dominance relationship. These cognitive models also imply differences in access to third-party information and other social information about the ranks of groupmates [71,72]. Theoretical models and agent-based simulations [73] present a promising venue to establish where models make different predictions about the dynamics of dyadic relationships. Empirically testing many of these models may require complete or nearly complete interaction data, so these tests are best suited for captive systems that support high-resolution data collection [64], potentially aided by automated data collection [74].

*When and why do dyads interact?*

Why do some dyads compete more than others? We know that in many species, attributes of dyads -- for instance, kinship, size similarity, or sex-homophily -- influence the frequency of agonistic interactions within dyads [75,76]. However, recent research also suggests that competition is sensitive to rank differences within dyads [71] – aggregated data on dominance interactions reveal rank-difference-based patterns in how animals engage in dyadic aggressive contests. This work suggests potential strategies determining when and why dyads choose to interact, inferred from these social dominance patterns. In the “downward heuristic” pattern, dyads interact at random with respect to rank differences. In contrast, in the “bullying” pattern, dyads with increasing rank differences are more likely to interact, and in the “close competitors” pattern, dyads with increasing rank differences are less likely to interact [71]. More work is needed to understand the processes that give rise to these patterns, how they change over time, and what they reveal about the dynamics of dyadic dominance relationships.

Interaction-to-relationship models (see previous section) are likely to make different predictions about the occurrence of these social dominance patterns. Newly formed groups of parakeets show unstructured aggression early after group-formation but quickly converge on the close competitor pattern, indicating how these patterns may reflect the process of dominance relationship formation [68]. A promising future direction is to inquire how interaction strategies combine with different interaction-to-relationship models to influence the stability of dyadic relationships and overall hierarchical stability (see next section). Are certain strategies more effective at ensuring the stability of dyadic relationships? For instance, under some interaction-to-relationship models, bullying the lowest-ranked group member is predicted to reinforce dyadic dominance relationships broadly with other group members, whereas under other models it is predicted to only influence the dyadic relationship of the bully and her target. Addressing this question will reveal how dyadic interaction strategies influence dominance hierarchy dynamics across scales.

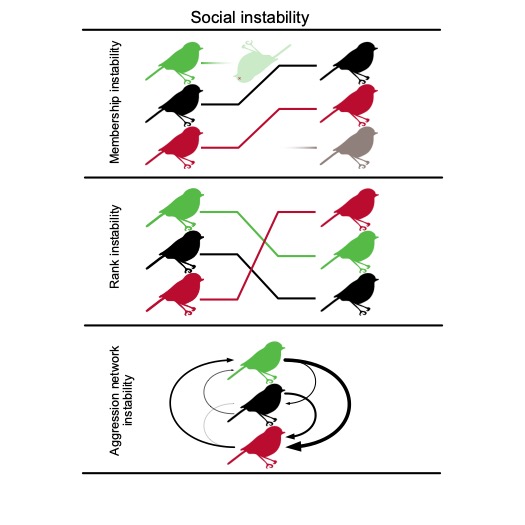
A challenge for understanding when and why dyads interact is that aggregated interaction data do not contain full information on the processes that influence dyadic interaction. These data only reflect interactions that occurred, but avoidance, long-distance signals, and behavioural state can influence how dyads interact by eliminating interactions [75,77]. Furthermore, dyadic interactions could be driven by the behaviour of the dominant or the subordinate member of the dyad (e.g., a subordinate approaching a dominant who is feeding), but agency over the interaction is often assumed to belong to the dominant individual. A solution to these problems is to incorporate data on these other covariates into analysis of dyadic interaction rate. For instance, accounting for spatial subgrouping in measures of the tendency for dyads to interact reflects interaction decisions after accounting for the opportunity to interact (Dehnen et al this issue). Incorporating data on the initiation of interactions (e.g., approaches) can reveal the extent to which dominant or subordinate individuals are influencing dyadic interaction rates. New analytical frameworks may be useful for incorporating multiple covariates into analyses of patterns of dyadic dominance interaction rates.

**Group level**

*What are the causes and consequences of social instability?*

Schjelderup-Ebbe hypothesized that dominance hierarchies serve to regulate conflict among group-members [1]. A corollary to this hypothesis is that social instability – i.e., changes to a social group’s dominance hierarchy – leads to increased conflict and its associated costs. Thus, an ongoing area of research is aimed at identifying periods of instability and determining the consequences of social instability for group members [78–80]. If instability is often not costly, this would challenge the idea that stable hierarchies arise as conflict regulatory adaptations [81]. Finally, there may be feedback between social instability and dominance-related traits, where competitive strategies differ in species with stable hierarchies compared to those with unstable hierarchies. For these reasons, to understand the role of dominance dynamics in animal societies, it is critical to explain the causes and consequences of social instability.

A major challenge to the study of social instability is to agree on what it is, what to call it, and how to measure it. In some studies, social instability is defined as a measure of changes in group composition [80,82,83], for instance due to the loss or gain of many individuals or the occurrence of group fission. In other studies, instability is defined by rearrangements of the dominance hierarchy or by changes in individual-level dominance rating over time [43,84,85]. Instability is also sometimes defined a third way, as a reduction in orderliness of the aggression network. Here, instability is measured by an increase in intransitivity in dominance relationships [79], or by an increase in the frequency and inconsistency of dominance interactions [86]. In order to properly understand sources of social instability and its impacts on animals, it is crucial to refine the concept to distinguish between these very different processes. We suggest distinguishing *membership instability* – caused by demographic turnover [62] -- from *rank instability*, caused by changes in the ordering of individuals in the hierarchy. Finally, *aggression network instability* is defined by an increase in uncertainty and intransitivity in aggression networks (Figure 2).



**Figure 2.** Three types of social instability. Membership instability results from demographic turnover. Rank instability results from rearrangements of the order of individuals within the social hierarchy. Aggression network instability results from a reduction in orderliness (e.g., transitivity, directional consistency) of the aggression network.

Distinguishing among these types of instability is especially important because they can interact in important ways. Demographic turnover can have direct effects on dominance hierarchies by removing or adding individuals and their relationships with others in the group, but can also have indirect effects on other individuals [62]. Influx of new individuals can lead to rank instability -- this is especially common in species with multi-male groups where males compete for dominance. For instance, during the mandrill mating season, an increased influx of males leads to increased intra-sexual competition, more active mobility among males and consequently higher rank instability, and higher levels of oxidative damage in high ranking males [78]. The loss of certain key individuals can also lead to rank instability [87] and aggression network instability [88], or even group collapse [89]. Membership instability, rank instability, or aggression network instability may be more impactful if it occurs in the upper echelons of the hierarchy [43,90]. Despite these avenues for interaction between types of social instability, it is also possible for each to occur independently of the others. Finally, extreme instability of these different types may occur rarely but have a large impact on animal societies, emphasizing the need to study these processes over long time-scales.

Methods exist for quantifying these different types of social instability, but again this is an area where there is room for improvement. To quantify membership instability, similarity metrics [91–93] can be used to assess differences in group composition between two time periods, even when group membership is not binary. Future work should aim to identify a metric that optionally weights measures of demographic turnover by the attributes (e.g., sex, rank) of individuals who join or leave the group. Multiple approaches exist for quantifying rank instability. One approach is to calculate an index based on the amount of active mobility taking place from one study period to the next. The S index [43] measures hierarchical instability in this way, but it has some shortcomings -- “study periods” have a fixed length of one day, mobility among highly-ranked individuals is weighted more heavily than others, and there is no way to account for measurement uncertainty. Future work should aim to extend this approach to assess instability over more biologically relevant time frames (Box 1; [49]), incorporate measurement uncertainty [39], and optionally weight instability among all individuals equally. Aggression network instability can be measured from the aggression network itself, for instance as frequency of the occurrence of intransitive triads [94] or the amount of uncertainty in the network [50]. However, doing so relies on the assumption that intransitivity reflects instability rather than a stable but intransitive state [79,81], an assumption which has received some support [65] and some criticism [95] and will likely vary by species. It could be productive to break the network into components and measure features of those components separately. For instance, the Helmholtz-Hodge decomposition can be used to break an aggression network into the sum of a unique perfectly transitive network and a unique perfectly cyclical network – aggression network instability can then be measured as the cardinality of the cyclical graph [96]. This approach could also allow for independent study of cyclical and transitive elements of the aggression network.

**Conclusion**

Despite a century of research, we still know surprisingly little about how and why dominance hierarchies change over time, and what impact these changes have on animal societies. Hierarchy dynamics occur at three scales – individual, dyadic, and group (Figure 1) – and open questions remain about the dynamics of dominance occurring at each of these scales. Although there are some challenges to addressing these questions, we suggest that solutions to these challenges are within reach (Table 1). In some cases, a lack of conceptual clarity is an ongoing challenge, and we present conceptual refinement to help overcome these issues and facilitate communication among researchers. In other cases, more work is needed to overcome the remaining challenges, and we suggest research directions that will advance the field. One critical need is to extend methods for inferring dynamics at the individual and group scales. These methods need to account for measurement uncertainty, and guidelines are needed for determining the time-scale at which to assess hierarchy dynamics. Fortunately, these are already active areas of research [29,43,49,97]. Models of optimal status-seeking behaviour and life history under different lifetime dominance trajectories will reveal how social mobility fits into the evolution of social traits. At the dyadic level, more work is needed to understand when and with whom individuals choose to interact [71], and how these interactions are integrated to form a relationship [65]. Here, a combination of model development and studies in captive groups provide a promising avenue for insight through an iterative process of model testing and refinement. Captive systems where high-resolution interaction data can be collected are promising systems in which to test different interaction-to-relationship models [64]. Across scales, systems where rank can be manipulated (e.g., Tung this issue) will be extremely useful for conducting targeted experiments testing hypotheses about the causes and consequences of the dynamics of dominance. Finally, long-term individual-based studies will be essential for interrogating dynamics occurring at long time scales and for studying the impact of rare events. Although much work remains to be done to better understand the dynamics of dominance in animal societies, the quality and quantity of ongoing work in this area suggests that insight into the structure and function of dominance hierarchies will continue into the next century.

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