The dynamics of dominance: open questions, challenges and solutions

Eli D. Strauss1,2,3,4 and Daizaburo Shizuka3

1Department of Collective Behavior, Max Planck Institute of Animal Behavior, Konstanz, Germany
2Centre for the Advanced Study of Collective Behaviour, University of Konstanz, Konstanz, Germany
3School of Biological Sciences, University of Nebraska Lincoln, Lincoln, NE, USA
4BEACON Center for the Study of Evolution in Action, Michigan State University, Lansing, MI, USA

Although social hierarchies are recognized as dynamic systems, they are typically treated as static entities for practical reasons. Here, we ask what we can learn from a dynamical view of dominance, and provide a research agenda for the next decades. We identify five broad questions at the individual, dyadic and group levels, exploring the causes and consequences of individual changes in rank, the dynamics underlying dyadic dominance relationships, and the origins and impacts of social instability. Although challenges remain, we propose avenues for overcoming them. We suggest distinguishing between different types of social mobility to provide conceptual clarity about hierarchy dynamics at the individual level, and emphasize the need to explore how these dynamic processes produce dominance trajectories over individual lifespans and impact selection on status-seeking behaviour. At the dyadic level, there is scope for deeper exploration of decision-making processes leading to observed interactions, and how stable but malleable relationships emerge from these interactions. Across scales, model systems where rank is manipulable will be extremely useful for testing hypotheses about dominance dynamics. 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.

This article is part of the theme issue ‘The centennial of the pecking order: current state and future prospects for the study of dominance hierarchies’.

1. Introduction

Dominance is one of the most widely 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 [1–3]. 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 [4]. Although the traditional static approach has produced valuable insight into the role of dominance in social systems, it sidesteps challenges associated with the dynamics of dominance, i.e. changes in dominance hierarchies over time. 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 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.
2. Individual level

(a) 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 [5–8]. For most species, it is unclear what causes individuals to change position in the dominance hierarchy, or conversely, how dominants may preserve their status [9,10]. It is important to understand the causes and consequences of rank changes [11], both to understand potential selection on status-seeking behaviour [12–14], and because rank changes can shed light on the forces involved in determining social rank in the first place [15,16]. 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 [17,18], rank reversal [19,20], revolutionary coalition [21], dominance turnover [22,23], social mobility [24–26] and power trajectories [27]. 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 between generations—intergenerational mobility—or within generations—intragenerational mobility [28]. Intergenerational mobility measures the extent to which parental
active mobility and intragenerational mobility that arise via different processes the hierarchy over their lifetimes. There are two types of intergenerational mobility describes movements of individuals in dominance rank predicts offspring dominance, whereas intragenerational mobility describes movements of individuals in the hierarchy over their lifetimes. 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, all remaining individuals improve their ranks by one position through passive intragenerational mobility [30,31]. Drivers of active mobility are less well-understood, but this type of mobility could result from changes in covariates that influence rank (e.g. increase in social support [12,15,32] or resource holding potential [22]), by stochastic outcomes that are reinforced (e.g. by winner/loser effects [33]), or feedbacks between multiple processes [34,35].

Recent work on hierarchy dynamics in spotted hyenas (Crocuta crocuta) illustrates the various forms of social mobility. In this system, social rank is highly predictable based on the rank of the mother, in a process termed ‘maternal-rank inheritance’, which is also observed in many old world monkeys [36–39]. Such systems represent an extreme version of restricted intergenerational mobility, because a female’s rank is strongly correlated with the rank of her mother. Intrigenerational mobility occurs through active and passive processes in this system. Active intragenerational mobility occurs when lower-ranking females overtake their higher-ranked groupmates through coalitionary support [15]. Passive intragenerational mobility owing to reproduction drives increasing differences among individuals and lineages over time [15]. This example demonstrates how 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.

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

Dominance rank is often linked to fitness [8], 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 [11,31,62], or they could be persistent and manifest even after individuals undergo social mobility [63]. 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 [8,10,64]. For instance, the costs of dominance status acquisition can offset the benefits of high rank [65–67], 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,
status-seeking behaviour and could lead subordinates to achieve high status by queuing, this relaxes selection on 
their ranks [41]. Theoretical work suggests that if subordinates can on-average tend to improve in social status over 
stability of social systems. For instance, some have suggested that an on-average tendency to improve in social status over 
dominance trajectories can reflect selection on status-seeking behaviour or influence the 
complexity to the ways that dynamic rank links to fitness.

Critical, 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 [41]. 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 [64]. 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 [35,70–72]. In summary, 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 [64] 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- versus intergenerational mobility, active versus passive mobility) [64,71]. For example, in systems where rank and fitness are highly correlated, and upward social mobility is largely passive, selection may favour 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 predomnates, selection may favour 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 [73–75]. In total, viewing dominance rank as a trajectory that unfolds over the life course will reveal typical 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 (or status-preserving, e.g. [76]) behaviour.

3. Dyadic level

(a) How do dominance relationships form and dissolve?

A century ago, Sjøldberg-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’ [1, p. 36]. Over a century of research on dominance, considerable progress has been made in understanding how the outcomes of interactions influence individual behaviour and physiology, but the dynamics of dyadic relationships are less well-understood. What processes lead some dominance relationships to form and persist, whereas others change, and still others are never formed?

A major insight from the last century of dominance research is that dominance relationships are influenced by the social context in which they operate—that is, dyadic dominance relationships are not determined in a vacuum, but are instead influenced by other dyadic relationships [77–79]. Dyads in newly formed groups tend to form dominance relationships producing transitive triads, demonstrating how the formation of relationships plays a causal role in shaping the formation of other relationships within the group [78,80,81]. A survey of dominance hierarchy structure across broad taxonomic groups confirms that this tendency towards transitive triads is a reliable feature of dominance hierarchies [82]. Most recently, work in chickens, cichlids and mice tracking all interactions among small newly formed groups provides an in-depth look into how dominance hierarchies emerge and persist after formation, showing that even after establishment, shifting dominance relationships still tend to change from one transitive network to another [56]. These results suggest that dominance hierarchies are best thought of as existing in a state of ‘dynamic stability,’ where dyadic relationships and individual positions in the hierarchy change but the overall transitive structural feature of the hierarchies remains constant. This impressive literature reveals why some dominance relationships are more likely to form than others, but we still do not know what processes produce the dynamics in dyadic relationships that give rise to this dynamic stability.

Individual and dyadic interaction history are processes that can contribute to the dynamics of dyadic dominance relationships. Theoretical and empirical work has demonstrated that dominance interactions lead to winner and loser effects, where the winners (losers) of interactions perceive themselves as more (less) able to win contests, and thus increase (decrease) their probability of winning subsequent interactions [33,83–85]. These winner- and loser-effects operate in addition to intrinsic differences in individual competitive ability to affect individual rank [86], but it is less clear how such effects impact dyadic relationships. Insofar as dominance relationships result from the combination of interactions [87,88], these effects of prior interaction experience are expected to influence dominance relationship formation [33]. However, in many species, individuals recognize groupmates, so dominance relationships formed between pairs of individuals are impacted by their specific dyadic interaction history [16,89–91]. When two individuals interact, the status of their dominance relationship is probed, reinforced or altered [87]. For unfamiliar individuals, repeated interactions quickly lead to the establishment of a dominance relationship, which is characterized by an overall reduction in aggression [92]. Repeated interactions can also lead to a change in how dominance relationships are assessed. For instance, in golden-crowned sparrows (Zonotrichia atricapilla), experimental enhancement of head plumage to signal higher dominance influenced dominance relationships among strangers but not among familiar flockmates, suggesting a move from reliance on status signals to recognition-based mechanisms of dominance relationship assessment [93]. In established relationships, additional interactions typically reinforce the existing dominance relationship, but can sometimes counter it and lead to its reversal. Individual-level changes such as winner/loser effects or changes in competitive ability play a role in the dynamics of these relationships, but are insufficient to fully explain these dyadic phenomena. Future work can shed new light on the evolution of dominance by exploring how individuals integrate information from prior interactions with specific opponents to form stable yet dynamic dyadic relationships.

Specifically, a productive way to deepen understanding of how dominance relationships form and dissolve requires the development of interaction-to-relationship models of how repeated interactions with particular opponents are integrated to form relationships [94]. 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 their determinants (e.g. body size, resource holding potential) suggest mechanisms by which stable dominance relationships might be pushed over a tipping point [34,95]. Interaction-to-relationship models need to consider: (i) potential time dependency in the influence of interactions on relationship status [96], (ii) effects of social context on the dyadic dominance relationship [78,79], and (iii) 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 [97], track the aggression received by group members and use it to infer position in the hierarchy [98], monitor aggression network structure using transitive inference [98],
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 [105,106]. Rank differences between individuals also shape interactions [76,107], for instance leading to increased likelihood of escalation of interactions among closely ranked individuals [108]. Recently, aggregated data on dominance interactions across a broad array of species has examined the occurrence of multiple rank-difference-based patterns of aggressive contests [101]. In the ‘downward heuristic’ pattern, dyads interact at random with respect to rank differences. By 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 [101]. This work suggests potential strategies determining when and why dyads choose to interact, inferred from these social dominance patterns. More work is needed to understand the processes that give rise to these patterns [107], 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 monk parakeets (Myiopsitta monachus) 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 [98]. 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 [109].

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 [105,110]. 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.

4. Group level

(a) What are the causes and consequences of social instability?

Schjelderup-Ebbe [1] hypothesized that dominance hierarchies serve to regulate conflict among group-members. 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 [111–113]. If instability is often not costly, this would challenge the idea that stable hierarchies arise as conflict regulatory adaptations [114]. 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, how to talk about it and how to measure it. In some studies, social instability is defined as a measure of changes in group composition [113,115,116], for instance owing 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 [47,52,117]. 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 [112], or by an increase in the frequency and inconsistency of dominance interactions [118]. Although thematically linked, these different types of instability do not necessarily arise from the same processes or have the same consequences. 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 different patterns. We suggest distinguishing membership instability—caused by
Finally, by changes in the ordering of individuals in the hierarchy. Instability, but again this is an area where there is room for processes over long time-scales. Different types may occur rarely but have a large impact on social instability, which can then be measured as the cardinality of the cyclical component of the network, or the amount of uncertainty in the network. However, doing so relies on the assumption that intransitivity reflects instability rather than a stable but intransitive state, an assumption which has received some support and some criticism and will probably 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. This approach could also allow for independent study of cyclical and transitive elements of the aggression network.

5. Conclusion

Dominance hierarchies are enigmatically both stable and dynamic. As a repeated pattern of asymmetry in agonistic outcomes between individuals, the concept of dominance is founded upon some element of stability. However, dominance relationships can also undergo rapid reversals, leading sometimes to dramatic changes in individual rank and group-level social instability. Nevertheless, even when relationships change, hierarchies gravitate towards the same underlying structural state of transitivity.

After a century of research on dominance hierarchies, we are still left with many questions to explore 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 (table 1). We have known for some time that individual ranks change over time (e.g. as individuals grow and age), but conceptual clarity about the different forms of social mobility will aid us in making sense of how evolution has moulded social traits and status-seeking behaviour in the context of life history. One critical need is to extend methods for inferring dynamics at the individual and group scales. These methods need to account for demographic turnover [75]—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 [57] (figure 2).

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 [75]. 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 (Mandrillus sphinx) 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 [111]. The loss of certain key individuals can also lead to rank instability [119,120] and aggression network instability [121], or even group collapse [122]. Membership instability, rank instability or aggression network instability may be more impactful if it occurs in the upper portion of the hierarchy [47,120]. Despite these avenues for interaction between types of social instability, it is also possible for each to occur independently of the others. Finally, in natural populations, extreme instability of these different types may occur rarely but have a large impact on animal societies [123], 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 [124–126] 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 weighs 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 [47] measures hierarchical instability in this way, but it has some shortcomings—"study periods" have a fixed length of 1 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; [55]), incorporate measurement uncertainty [45], 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 [82] or the amount of uncertainty in the network [58]. However, doing so relies on the assumption that intransitivity reflects instability rather than a stable but intransitive state [112,114], an assumption which has received some support and some criticism and will probably 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 [128]. This approach could also allow for independent study of cyclical and transitive elements of the aggression network.

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. (Online version in colour.)
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 [29,47,55,129]. At the dyadic level, more work is needed to understand when and with whom individuals choose to interact [101], and how these interactions are integrated to form a relationship [94]. 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 groups where high-resolution interaction data can be collected are promising systems in which to test different interaction-to-relationship models [56,92]. Across scales, study systems where rank can be manipulated (e.g. [62]) will be extremely useful for conducting targeted experiments testing hypotheses about the causes and consequences of the dynamics of dominance. There is also room for work integrating studies of the dynamics of dominance with other forms of social power [130]. Finally, long-term individual-based studies will be essential for interrogating dynamics occurring at long timescales and for studying the impact of rare events. We hope that this research agenda enables new insight into the dynamics of dominance and further extends the last century of productive research into this fundamental dimension of social organisms.

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References

1. Schjelderup-Ebbe T. 1975 Contributions to the social psychology of the domestic chicken (M. Schiedt, WM Schiedt, translators). In Social hierarchy and dominance. Benchmark papers in animal behavior, vol. 3 (ed. MW Schein). pp. 35–49. Stroudsburg, PA: Dowden, Hutchinson & Ross. (Reprinted from Reprod. Z. Psychol. 1922, 88, 225–252.)
2. Strauss ED, DeCasien AR, Galindo G, Hobson EA, Shizuka D, Curley JP. 2022 DomArchives: a century of published dominance data. Phil. Trans. R. Soc. B 377, 20200436. (doi:10.1098/rstb.2020.0436)
3. Hobson EA. 2022 Quantifying the dynamics of nearly 100 years of dominance hierarchy research. Phil. Trans. R. Soc. B 377, 20200431. (doi:10.1098/rstb.2020.0433)
4. Holekamp KE, Strauss ED. 2016 Aggression and dominance: an interdisciplinary overview. Curr. Opin. Behav. Sci. 12, 44–51. (doi:10.1016/j.cobeha.2016.08.005)
5. Snyder-Mackler N et al. 2020 Social determinants of health and survival in humans and other animals. Science 368, eaax9553. (doi:10.1126/science.aax9553)
6. Sapolsky RM. 2005 The influence of social hierarchy and dominance on health and survival in humans and other animals. Science 368, eaax9553. (doi:10.1126/science.aax9553)
7. Majolo B, Lehmann J, De Bortoli Vizioli A, Schino G. 2011 Reluctant challenges: why do subordinate female meerkats rarely displace their dominant mothers? Behav. Ecol. 22, 1337–1343. (doi:10.1093/beheco/arr138)
8. Ellis L. 1995 Dominance and reproductive success among nonhuman animals: a cross-species comparison. Ethol. Sociobiol. 16, 257–333. (doi:10.1016/0162-3095(95)90050-4)
9. Sharp SP, Clutton-Brock TH. 2011 Reluctant challengers: why do subordinate female meerkats rarely displace their dominant mothers? Behav. Ecol. 22, 1337–1343. (doi:10.1093/beheco/arr138)
10. Van Schaik C, Van Noordwijk M. 2001 Career moves: transfer and rank challenge decisions by male long-tailed macaques. Behaviour 138, 359–395. (doi:10.1163/15685390152032505)
11. Wallace KJ, Choudhary KD, Kutty LA, Le DH, Lee MT, Wu K, Hoffmann HA. 2022 Social ascent changes cognition, behaviour and physiology in a highly social cichlid fish. Phil. Trans. R. Soc. B 377, 20200448. (doi:10.1098/rstb.2020.0448)
12. Schulke O, Bhagavatula J, Vigilant L, Ostner J. 2010 Social bonds enhance reproductive success in male macaques. Curr. Biol. 20, 2207–2210. (doi:10.1016/j.cub.2010.08.058)
13. Young C, Majolo B, Schulke O, Ostner J. 2014 Male social bonds and rank predict supporter selection in cooperative aggression in wild Barbary macaques. Anim. Behav. 95, 23–32. (doi:10.1016/j.anbehav.2014.06.007)
14. Van Schaik CP, Pandit SA, Vogel ER. 2004 A model for within-group coalitionary aggression among males. Behav. Ecol. Sociobiol. 57, 101–109. (doi:10.1007/s00265-004-0818-1)
15. Strauss ED, Holekamp KE. 2019 Social alliances improve rank and fitness in convention-based societies. Proc. Natl. Acad. Sci. USA 116, 8919–8924. (doi:10.1073/pnas.1803841116)
16. Tibbetts EA, Pardo-Sanchez J, Weise C. 2022 The establishment and maintenance of dominance hierarchies. Phil. Trans. R. Soc. B 377, 20200450. (doi:10.1098/rstb.2020.0450)
17. Samuels A, Silk JB, Altmann J. 1987 Continuity and change in dominance relations among female baboons. Anim. Behav. 35, 785–793. (doi:10.1016/S0003-3472(87)80115-X)
18. Gouzoules H. 1984 A description of genealogical rank changes in a troop of Japanese monkeys (Macaca fuscata). Primates 25, 262–267. (doi:10.1007/BF02374039)
19. Chapais B. 1985 An experimental analysis of a mother-daughter rank reversal in Japanese macaques (Macaca fuscata). Primates 26, 407–423. (doi:10.1007/BF02382465)
20. Perry S. 1998 A case report of a male rank reversal in a group of white-faced capuchins (Cebus capucinus). Primates 39, 51–70. (doi:10.1007/BF02557743)
21. Higham J, Maestripieri D. 2010 Revolutionary coalitions in male rhesus macaques. Behaviour 147, 1889–1908. (doi:10.1163/000579510X539709)
22. Hasegawa M, Kutsukake N. 2014 Bayesian competitiveness estimation predicts dominance turnover among wild male chimpanzees. Behav. Ecol. Sociobiol. 69, 89–99. (doi:10.1007/s00265-014-1821-9)
23. Kutsukake N, Hasegawa T. 2005 Dominance turnover between an alpha and a beta male and dynamics of social relationships in Japanese macaques. Int. J. Primatol. 26, 775–800. (doi:10.1007/107676-005-5308-4)
24. Dettmer AM, Woodward RA, Suomi SJ. 2015 Reproductive consequences of a multilinear overthrow in rhesus monkeys. Am. J. Primatol. 77, 346–352. (doi:10.1002/ajp.22150)
25. Gates-O’Brien RS, Farver TB, Anderson-Vicino KC, McGowan B, Leche NW. 2010 Predictors of multilinear overthrows in large captive breeding groups of rhesus macaques (Macaca mulatta). J. Assoc. Lab. Anim. Sci. 49, 196–201.
26. Ehardt CL, Bernstein IS. 1986 Matrilineal overthrow in rhesus monkey groups. Int. J. Primatol. 7, 157–181. (doi:10.1007/BF02692316)
27. Young C, McFarland R, Barrett L, Henzi SP. 2017 Formidable females and the power trajectories of socially integrated male vervet monkeys. Anim. Behav. 125, 61–67. (doi:10.1007/j.anbehav.2017.01.006)
cooperative breeder. *Anim. Behav.* **146**, 113–122. (doi:10.1016/j.anbehav.2018.10.013)

72. Barve S, Hagemeier NG, Winter RE, Chamberlain SD, Koenig WD, Winkler DW, Walters EL. 2020. Wandering woodpeckers: foray behavior in a social bird. *Ecology* **101**, 1–8. (doi:10.1002/ecy.2943)

73. Armassini NC, Staw AJ, Cantor M, Leu ST, Klarevas-Irby JA, Charlton AA, Farine DR. 2020. Social barriers in ecological landscapes: the social resistance hypothesis. *Trends Ecol. Evol.* **35**, 137–148. (doi:10.1016/j.tree.2019.10.001)

74. Silk MJ, Hodgson DJ. 2021. Differentiated social relationships and the pace-of-life history. *Trends Ecol. Evol.* **36**, 498–506. (doi:10.1016/j.tree.2021.02.007)

75. Shizuka D, Johnson AE. 2020. How demographic processes shape animal social networks. *Behav. Ecol.* **31**, 1–11. (doi:10.1093/beheco/azt083)

76. Hamilton IM, Benincasa MD. 2022. Emergence of size-structured dominance hierarchies through size-dependent feedback. *Phil. Trans. R. Soc. B* **377**, 20200449. (doi:10.1098/rstb.2020.0449)

77. Chase ID. 1974. Models of hierarchy formation in animal societies. *Behav. Sci.* **19**, 374–382. (doi:10.1002/bbs.3380190604)

78. Chase ID. 1985. The sequential analysis of aggressive acts during hierarchy formation: an application of the ‘jigsaw puzzle’ approach. *Anim. Behav.* **33**, 86–100. (doi:10.1016/0003-3472(85)80122-6)

79. Chase ID, Tovey C, Manfredonia J. 2018. The fragility of dominance hierarchies in a wild primate population. *Proc. R. Soc. B* **285**, 20180445. (doi:10.1098/rspb.2018.0445)

80. Chase ID, Tovey C, Spangler-Martin D, Manfredonia J. 2019. Hierarchical classification by rank and kinship in baboons. *Science* **362**, 1234–1236. (doi:10.1126/science.1087513)

81. Karavanič C, Atima J. 1998 Individual recognition and memory in lobster dominance. *Anim. Behav.* **56**, 1553–1560. (doi:10.1006/anbe.1998.0914)

82. Pevney JL, Barnard K. 2022. The sequential analysis of aggressive acts during hierarchy formation in mice. *PLoS ONE* **17**, e0220596. (doi:10.1371/journal.pone.0220596)

83. Chase ID, Tovey C, Spangler-Martin D, Manfredonia J. 2019. Temporal microstructure of dyadic social behavior during relationship formation in mice. *PLoS ONE* **14**, e0220596. (doi:10.1371/journal.pone.0220596)

84. Mesterton-Gibbons M. 1999. On the evolution of winner-loser models of hierarchy formation in ecological landscapes. *J. Exp. Biol.* **202**, 836–848. (doi:10.1242/jeb.18)

85. Maldonado-Chaparro AA, Alarcón-Nieto G, Klarevas-Irby JA, Farine DR. 2018. Experimental disturbances reveal group-level costs of social instability. *Proc. R. Soc. B* **285**, 20180536. (doi:10.1098/rspb.2019.0536)

86. Hamilton IM, Heg D, Bender N. 2005. Size differences within a dominance hierarchy influence conflict and help in a cooperatively breeding cichlid. *Behaviour* **142**, 1591–1613. (doi:10.1163/156853905774381846)

87. Sosa S. 2016. The influence of gender, age, matriline and hierarchical rank on individual social position, role and interactional patterns in macaca sylvanus at ‘La Forêt des Singes’: a multilevel social network approach. *Front. Psychol.* **7**, 1–12. (doi:10.3389/fpsyg.2016.00529)

88. Drewe C. 1993. The concept and definition of dominance in animal behaviour. *Behaviour* **125**, 283–313. (doi:10.1163/156853993X00290)

89. Hinde RA. 1976. Interactions, relationships and social structure. *Am. J. Primatol.* **5**, 365–379. (doi:10.1002/ajp.1330050406)
119. Wooddell LJ, Kaburu SSK, Rosenberg KL, Meyer JS, Suomi SJ, Dettmer AM. 2016 Matrilineal behavioral and physiological changes following the death of a non-alpha matriarch in rhesus macaques (Macaca mulatta). PLoS ONE 11, e0157108. (doi:10.1371/journal.pone.0157108)

120. Piefke TJ, Bonnell TR, Deoliveira GM, Border SE, Dijkstra PD. 2021 Social network stability is impacted by removing a dominant male in replicate dominance hierarchies of a cichlid fish. Anim. Behav. 175, 7–20. (doi:10.1016/j.anbehav.2021.02.012)

121. Flack JC, Girvan M, De Waal FBM, Krakauer DC. 2006 Policing stabilizes construction of social niches in primates. Nature 439, 426–429. (doi:10.1038/nature04326)

122. Beisner BA, Jin J, Hsieh F, Mccowan B. 2015 Detection of social group instability among captive rhesus macaques using joint network modeling. Can. Zool. 61, 70–84. (doi:10.1093/czoolo/61.1.70)

123. Sapolsky RM, Share L. 2004 A pacific culture among wild baboons: Its emergence and transmission PLoS Biol. 2, e106. (doi:10.1371/journal.pbio.0020106)

124. Jaccard P. 1912 The distribution of the flora in the alpine zone. New Phytol. 11, 37–50. (doi:10.1111/j.1469-8137.1912.tb05611.x)

125. Levandowsky M, Winter D. 1971 Distance between sets. Nature 234, 34–35. (doi:10.1038/234034a0)

126. Bray JR, Curtis JT. 1957 An ordination of the upland forest communities of Southern Wisconsin. Ecol. Monogr. 27, 325–349. (doi:10.2307/1942268)

127. Douglas PH, Ngonga Ngomo AC, Hohmann G. 2017 A novel approach for dominance assessment in gregarious species: ADAGIO. Anim. Behav. 123, 21–32. (doi:10.1016/j.anbehav.2016.10.014)

128. Strang A, Abbott KC, Thomas PJ. 2020 The network hhd: quantifying cyclic competition in trait-performance models of tournaments. arXiv, 2011.01825.

129. Williamson CM, Lee W, Cutley JP. 2016 Temporal dynamics of social hierarchy formation and maintenance in male mice. Anim. Behav. 115, 259–272. (doi:10.1016/j.anbehav.2016.03.004)

130. Lewis RJ. 2022 Aggression, rank and power: why hens (and other animals) do not always peck according to their strength. Phil. Trans. R. Soc. B 377, 20200454. (doi:10.1098/rstb.2020.0434)