How feedback and feed-forward mechanisms link determinants of social dominance

Authors

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Abstract

In many animal societies, individuals differ consistently in their ability to win agonistic interactions, resulting in dominance hierarchies. These differences arise due to a range of factors that can influence individuals' abilities to win agonistic interactions, spanning from genetically driven traits through to individuals' recent interaction history. Yet, despite a century of study since Schjelderup-Ebbe's seminal paper on social dominance, we still lack a general understanding of how these different factors work together to determine individuals' positions in hierarchies. Here, we first outline five widely studied factors that can influence interaction outcomes: intrinsic attributes, resource value asymmetry, winner-loser effects, dyadic interaction-outcome history and third-party support. A review of the evidence shows that whilst different factors have been shown to be important in specific systems, there are few empirical cases where one factor has a definitive effect. We then propose that mixed empirical support for a single factor is likely to arise due to feedback loops, whereby the outcomes of previous agonistic interactions (e.g. access to food) impact factors that might be important in subsequent interactions (e.g. body condition). We provide a conceptual framework which illustrates that there are many potential routes through which feedbacks can occur. Such feedbacks suggest that the factors that determine outcomes of dominance interactions are highly intertwined and are likely to rarely act independently of one-another. Further, we generalise our framework to include multi-generational feed-forward mechanisms and highlight how interaction outcomes in one generation can influence the factors determining interaction outcomes of their offspring via a range of parental effects. This general framework describes how interaction outcomes and the factors determining them are linked within generations via feedback loops, and between generations via feed-forward mechanisms. We then highlight methodological approaches that will facilitate the study of feedback loops and dominance dynamics. Lastly, we discuss how our framework can shape future research, including investigating how feedbacks in dominance hierarchies produce 'self-organised' structure, exploring how interaction outcomes are integrated to form dominance hierarchies, and the routes of parental influence on the dominance status of offspring. Ultimately, by considering dominance interactions as part of a dynamic system, that also feeds forward into subsequent generations, we will better understand the factors that structure dominance hierarchies in animal groups.

Key words: social dominance, feedback loops, group living, hierarchy, parental effects, competition, agonistic interactions

Contents

I. Introduction

Living in groups is widespread among animals and has many benefits including access to information, cooperative foraging and enhanced predator detection. However, animals that live in groups also experience enhanced costs such as increased competition for resources, which often leads to aggressive encounters among group-members (Ward & Webster, 2016). It is typical that individuals differ in their tendency to win such agonistic interactions, and therefore for some individuals to be socially dominant over others (Holekamp & Strauss, 2016). Such dyadic dominance relationships among group members give rise to group-level patterns known as dominance hierarchies. These are a prominent feature of the social structure of many group-living species, including invertebrates, fish, birds and mammals (Shizuka & McDonald, 2012).

Social dominance is known to have far-reaching consequences. For example, having a higher position in the dominance hierarchy generally translates to greater access to resources—such as food (see Ward & Webster, 2016), mating opportunities (Ellis, 1995), and preferential positions in roosts (McGowan *et al.*, 2006). Therefore, social dominance can have fitness, and subsequently evolutionary, consequences (Clutton-Brock, 1988; Snyder-Mackler *et al.*, 2020). Furthermore, dominance status is related to many other aspects of biology, such as physiology (Sapolsky, 2005), gene expression (So *et al.*, 2015) and the dynamics of group movements (Papageorgiou & Farine, 2020). Thus, understanding the causes and consequences of dominance has far-reaching implications.

Social dominance has received considerable research attention, with numerous theoretical (e.g. Beacham 2003; Kura, Broom, and Kandler, 2016) and empirical (e.g. Lindquist & Chase, 2009; Strauss & Holekamp, 2019a) studies, as well as reviews (e.g. Hsu, Earley, & Wolf, 2006; Holekamp & Strauss, 2016), published since dominance hierarchies were first described a century ago (Schjelderup-Ebbe, 1922). This plethora of studies has yielded many hypothesised factors that can influence individuals' abilities to win contests with conspecifics and, thereby, the direction of dyadic dominance relationships – ultimately dictating individuals' positions in the hierarchy. Among these are individuals' physical attributes (Chase *et al.*, 2002), winner-loser effects (Hsu *et al.*, 2006), dyadic interaction-outcome history (Chaine *et al.*, 2018), resource-value asymmetries among contesting individuals (Smith & Parker, 1976), and third-party support (Schülke *et al.*, 2010). However, there is a distinct lack of integration between different approaches to dominance, as particular factors are central to one approach yet absent in others. For example, resource value is central to game theory but absent in studies of hierarchy structure (Parker, 1974; Smith & Parker, 1976; Chase *et al.*, 2002). Furthermore, factors affecting interaction outcomes are often considered as competing hypotheses (Chase *et al.*, 2002; Holekamp & Strauss, 2016), whereas it is likely that a combination of multiple factors determines the outcome of a particular interaction.

As with state-behaviour feedback in other areas of ecology (Sih *et al.*, 2015), the different drivers of interaction outcomes are unlikely to act in isolation. Drivers may change over time and, importantly, are likely to interact with one another via feedback loops. In addition, parents can influence the factors determining offspring interaction outcomes, and thereby dominance status, via various routes. Thus, within-generation feedback loops also feed into the next generation via mechanisms such as maternal effects, parental support in agonistic interactions and social inheritance of parental social bonds. Our understanding of dominance hierarchies will undoubtedly benefit from integrating the complex interplay between interaction outcomes and the myriad of factors—both within and across generations—that influence them.

To date, an overarching framework, which integrates the many potential factors involved in structuring dominance relations in wild populations, remains absent (Holekamp & Strauss, 2016). Here, we aim to unify different approaches and provide a complete overview of the processes that shape and maintain dominance relationships in natural populations. First, we outline the various factors hypothesised and shown to contribute to interaction outcomes between individuals. Next, we describe how different factors that influence interaction outcomes are linked via feedback loops. We go on to describe ways in which parents can influence the factors affecting interaction outcomes in their offspring, thus placing these factors determining and their feedback loops into a broader conceptual framework that includes transgenerational parental effects. Then, we suggest some methodological approaches that may allow the study of feedback loops and hierarchy dynamics. Lastly, we point out emerging questions and suggest new research avenues for empiricists interested in studying the dynamics of dominance and its determinants.

II. Factors that determine interaction outcomes

(1) Intrinsic attributes

The literature on dominance hierarchy structure often focuses on how ‘prior attributes’, characteristics such as sex, size or strength, affect interaction outcomes (Chase *et al.*, 2002). However, it is often unclear whether ‘prior’ refers to attributes (i) before a particular interaction versus (ii) before a group is formed (e.g. in experimental studies, Chase *et al.*, 2002) and *any* dominance interactions occur among its members. The latter scenario is problematic because dominance hierarchies in natural animal groups, aside from those in broods or litters (Drummond, 2006), typically do not form *de novo* and can persist for many generations (e.g. Strauss & Holekamp, 2019a). Additionally, interpretation (ii) implies that ‘prior’ attributes remain unchanged over time, which is rarely the case. For example, body mass varies with changing resource access (Polo & Bautista, 2002), while skeletal size increases throughout development until adult size is reached. Similarly, fighting ability can be reduced instantaneously as a result of injuries (Clutton-Brock *et al.*, 1979), or gradually improve with increasing experience (Sih *et al.*, 2015). Moreover, some traits, such as personality, that are considered to be relatively static in isolation (Sih, Bell, & Johnson, 2004) can be influenced by social context (Jolles, Taylor, & Manica, 2016). Thus, virtually all ‘prior’ attributes are likely to be dynamic in some form. Accordingly, to avoid such problems with the term ‘prior attributes’, we suggest the use of ‘intrinsic attributes’ instead (Beacham, 2003) and refer to them as such here.

Intrinsic attributes are rarely effective in isolation of other traits. Typically, single measures such as size, mass, length or height, are used as a proxy for *all* intrinsic attributes that affect interaction outcomes, by relating the trait to winning propensity or hierarchy position (Wilson, 1975; Clutton-

Brock *et al.*, 1979; Beaugrand, Payette, & Goulet, 1996; Chase *et al.*, 2002; Archie *et al.*, 2006; Mitchem *et al.*, 2019; see also Table 2 in Hsu *et al.*, 2006). Intrinsic attributes that affect interaction outcomes may, however, encompass a broad range of perhaps less obvious traits, such as testosterone levels (Schwabl, 1993), personality (Riebli *et al.*, 2011; Mitchem *et al.*, 2019) and fighting skills (Briffa & Lane, 2017). Importantly, many unmeasured intrinsic attributes can affect the outcomes of dominance interactions, which is a central problem to designing experiments that aim to disentangle multiple factors (Chase *et al.*, 2002). Furthermore, because position in a dominance hierarchy often influences access to food resources, which can in turn influence intrinsic attributes (e.g. Richner, 1992), causality in a positive relationship between an intrinsic attribute and dominance cannot be assumed. Thus, while there are cases where intrinsic attributes appear to have a strong predictive effect on interaction outcomes (see Table 2 in Hsu *et al.*, 2006) instances where intrinsic attributes are the sole contributing factor are likely to be exceptions rather than the rule.

(2) Resource-value asymmetry

The value of a contested resource to an individual influences its contest investment and, thereby, can affect interaction outcomes that occur over resources. Here, we refer to ‘resource value’ as the net value of a resource to an individual – this being the benefits minus the costs of gaining (or retaining) access to the resource. Accordingly, resource-value asymmetry is the difference in resource value between two individuals competing for a given resource. Game-theoretic approaches have long considered differences in the value of a contested resource between competing individuals to influence contest outcomes (Smith & Parker, 1976). Resource-value asymmetries occur in various contexts, such as when competing over food (Cristol, 1992), mates (Ancona, Drummond, & Zaldívar-Rae, 2010) or territories (Bergman, Olofsson, & Wiklund, 2010). Nevertheless, while resource-value asymmetries have been suggested to affect dominance hierarchy structure (Hsu *et al.*, 2006), they remain largely ignored by most studies of dominance (Holekamp & Strauss, 2016).

An asymmetry in resource value among two competing individuals will generally influence the contest outcome because animals competing for resources that are more valuable to them should increase contest investment, i.e. be more aggressive, incur larger costs or greater risks (Enquist & Leimar, 1987; Arnott & Elwood, 2008). For example, in whiptail lizards *Aspidoscelis costata*, males defending larger (and thus more valuable) females were more aggressive (Ancona *et al.*, 2010). Differences in resource value between competing individuals are also likely to arise due to individuals' different contexts. For example, in blue–black grassquit *Volatinia jacarina* males contesting a food resource, individuals in poorer body condition were more aggressive, and thus more dominant, than those in better condition (Santos, Maia, & Macedo, 2009). Furthermore, male house crickets *Acheta domesticus* that had no prior access to females, relative to males that did, showed increased aggression when competing for a female (Brown, Chimenti, & Siebert, 2007). Asymmetries in resource value between contesting individuals also occur when competing for resources that are occupied—rather than depleted—by the resource owner, such as in owner-intruder contexts. Typically, the individual in possession of the contested commodity has more to lose (i.e. a higher resource value) than an intruder, which usually results in 'owners' winning disproportionately more contests (Smith & Parker, 1976; Enquist & Leimar, 1987). Examples of this include resident male snow skinks *Niveoscincus microlepidotus* competing for burrows winning over 70% of contests (Olsson & Shine, 2000); nest-owning European paper wasps *Polistes dominula* being more aggressive than intruders when competing for nests (Injaian & Tibbetts, 2015); and male cichlids *Neolamprologus pulcher* being more aggressive with increased resource value (in territorial contests) and therefore more likely to win contests (O'Connor *et al.*, 2015). Accordingly, it is the objective value of a resource *modulated by* the contexts in which both individuals are competing that determines contest investment. Subsequent differences in contest investment due to resource-value asymmetry between two competing individuals (in combination with the other factors in section II) are then likely to dictate the extent to which resource-value asymmetry influence the outcome of an interaction.

It is important to note that, when the contested resource is food, some factors may be considered to be in both the intrinsic attribute *and* resource value category. For example, body fat percentage, and the associated survival benefit that food brings, can determine resource value—and thus resource-value asymmetry—yet body fat percentage is also an intrinsic attribute that may affect competitive ability. Accordingly, intrinsic attributes and resource-value asymmetries are often strongly linked.

(3) Winner-loser effects

Winner-loser effects predict that individuals who won their most recent contest experience an increased probability of winning their next contest, while in those that lost their most recent contest, this probability is reduced (McDonald, Heimstra, & Damkot, 1968; Hsu *et al.*, 2006; Rutte, Taborsky, & Brinkhof, 2006). Evidence for winner-loser effects comes predominantly from experimental and captive settings, but spans across invertebrates (Trannoy *et al.*, 2016), fish (Chase *et al.*, 2002), reptiles (Schuett, 1997), birds (Martin, Beaugrand, & Laguë, 1997) and mammals (Huhman *et al.*, 2003). In part, this lack of evidence from wild populations is likely due to the challenge of observing continuous interaction outcomes across time. However, recent work on savannah baboons provides important observational support for winner-loser effects in a wild system (Franz *et al.*, 2015).

An important feature of winner-loser effects is that they are thought to act regardless of opponent identity (Rutte *et al.*, 2006). As a result, winner-loser effects have often been studied in the context of the social dynamics hypothesis, which posits that hierarchies are ‘self-organising’ and that a linear hierarchy structure arises due to such effects in the absence of other influences, such as the effects of intrinsic attributes (Chase *et al.*, 2002). However, studies of winner-loser effects are typically conducted in laboratory settings, where natural variation in other important factors (e.g. size, an intrinsic attribute) can be minimised, studies are of a short duration, and tend to focus only on newly formed groups within a single generation (McDonald *et al.*, 1968; Beacham, 1988; Chase *et al.*, 2002; Dugatkin & Druen, 2004; Laskowski, Wolf, & Bierbach, 2016). Such studies therefore remove many of the additional factors that potentially influence contest outcomes in natural populations. Thus, while their existence is well established, the broader importance of winner-loser effects, especially in conjunction with other factors, to wild animal groups remain unclear.

The effect of a *single* win or loss on future wins or losses tends to last only for very short timespans—hours to days (Kasumovic *et al.*, 2010; Trannoy *et al.*, 2016). However, providing that interactions occur relatively frequently, an individual's winner/loser state influences the outcome of a subsequent interaction which in turn affects that individual's winner/loser state. Therefore, winner-loser effects, at least in isolation, can cause a runaway positive feedback and thereby act as a stabilising mechanism to dominance hierarchies (i.e. all else being equal, losers keep losing and winners keep winning Rutte *et al.*, 2006). Such *continued* winning or losing, as is likely to occur in natural populations where individuals interact frequently, can have longer-lasting effects (Trannoy *et al.*, 2016) and even influence later-life dominance relationships (Laskowski *et al.*, 2016). Given that winner-loser effects typically last for only hours to days (Hsu *et al.*, 2006), the importance of winner and loser effects likely depends on the duration that the effects last relative to the rates at which individuals engage in dominance interactions. Thus, they could be particularly important in species where repeated interactions take place, or those in which interactions precipitate subsequent interactions in quick succession.

(4) Dyadic interaction-outcome history

In species with relatively stable group membership and small group sizes, individuals can recognise group members individually and thus establish stable, dyadic dominance relationships (Drews, 1993). When established dominance relationships exist, individuals do not usually engage in escalated contests, but subordinates simply acknowledge existing dominance relationships via unprovoked submissive interactions (Holekamp & Smale, 1991). The dyadic interaction-outcome history is likely to influence interactions across a wide range of species, even those that use status badges to estimate relative dominance. For example, in golden-crowned sparrows *Zonotrichia atricapilla*, manipulation of status-signalling badges influenced the direction of dominance in pairs of strangers but, critically, not between familiar flock mates (Chaine *et al.*, 2018). Familiarity between opponents can also change the magnitude of the aggression displayed. For example, in pairs of contesting green anoles *Anolis carolinensis*, losers of an initial interaction were significantly less aggressive when repaired with their previous opponent, relative to being paired with an unknown individual (Forster *et al.*, 2005), while in rainbow trout *Oncorhynchus mykiss*, aggression in contests among familiar individuals was lower than among unfamiliar individuals (Johnsson, 1997). These studies demonstrate that prior interaction outcomes influence subsequent interactions outcomes in the same dyad. Such modulation of agonistic behaviour based on previous dyadic interaction outcomes, facilitated by individual recognition (Barnard & Burk, 1979; Tibbetts & Dale, 2007), allows individuals to avoid engaging in potentially costly contests which they are unlikely to win.

(5) Third-party support

In many species, third-party individuals can influence the outcomes of dyadic interactions. This often occurs in the form of parental (typically maternal) support to offspring (Engh *et al.*, 2000), support provided after the formation of an alliance (Smith *et al.*, 2010) or traded as a commodity for other services (Borgeaud & Bshary, 2015). Importantly, third-party individuals may influence dyadic interaction outcomes simply by being present, without directly intervening in ongoing contests (Holekamp & Smale, 1991). The third-party support discussed in this section can allow individuals to 'tip the scales' of factors determining interaction outcomes in their favour, allowing them to ascend the dominance hierarchy (Strauss & Holekamp, 2019a).

(a) Parental support

Extended parent-offspring associations occur in many species and allow parents, typically mothers, to support offspring during agonistic interactions (Holekamp & Smale, 1991). Usually, parental support—such as defensive maternal intervention on behalf of their offspring, or mothers joining their offspring in aggression against a particular opponent—increases the probability of offspring winning a dominance interaction (see Holekamp & Smale, 1991). Empirical examples come predominantly from primates (for review see Maestripieri, 2018) and spotted hyenas *Crocuta crocuta* (see Holekamp & Smale, 1993). However, parental support has also been shown to be important to dominance interactions in birds, such as Bewick's swans *Cygnus columbianus bewickii*, where parental absence profoundly reduces the probability of cygnets winning agonistic interactions (Scott, 1980). Accordingly, parental intervention can be an important force in shaping interaction outcomes (Holekamp & Strauss, 2016), with the effects potentially being more or less obvious across different species.

(b) Social support

Third-party support can also be provided by non-parent individuals, which we here refer to as 'social support'. Such support in agonistic interactions is not uncommon in group-living species with pronounced dominance hierarchies (Smith *et al.*, 2010; Maestripieri, 2018), and appears to be particularly commonly found in primates. For example, chacma baboons *Papio ursinus* can form aggressive alliances with other, unrelated individuals such as members of more dominant matrilines (Cheney, 1977); vervet monkeys *Chlorocebus pygerythrus* provide support in agonistic encounters in exchange for grooming services (Borgeaud & Bshary, 2015); and male chimpanzees *Pan troglodytes schweinfurthii* form coalitions in agonistic encounters, and do so increasingly with age (Enigk *et al.*, 2020). Social support also occurs in birds. For example, ravens *Corvus corax* intervene in on-going agonistic interactions to support close associates (Fraser & Bugnyar, 2012). Third-party individuals may not need to intervene directly to influence interaction outcomes – as is the case in spotted hyenas where the individual with greater *recruitable* social support usually wins the focal agonistic interaction (Vullioud *et al.*, 2019). Because many species in which social support has been studied are highly kin-structured or have nepotistic dominance hierarchies, it has most commonly been reported to be preferentially kin-directed (e.g. Surbeck, Mundry, & Hohmann, 2011). However, social support could also occur, albeit more subtly, in other situations, such as in species where individuals form strong pair bonds. For example, the presence of a dominant mate might prevent aggressive interactions being directed to the partner (Wechsler, 1988). While evidence for individuals directly intervening in ongoing interactions on behalf of a social partner is scarce, if not absent, more targeted research could reveal social support via reduced aggression as opposed to direct, physical interventions.

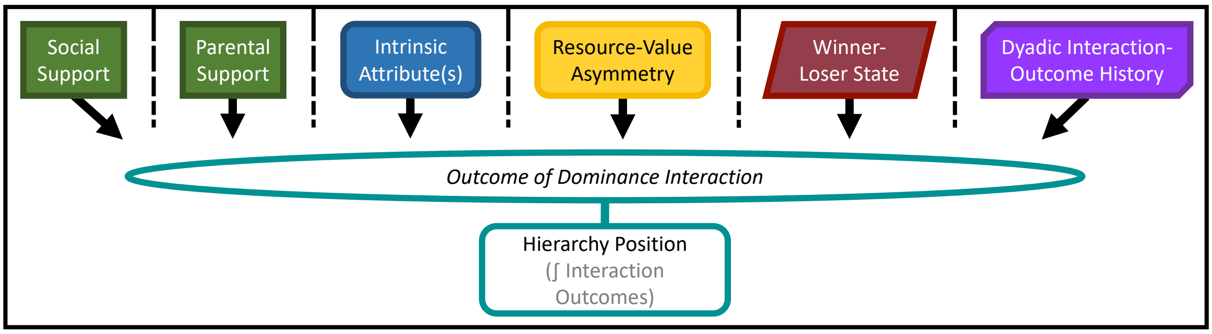

Fig. 1. Six potential factors (filled boxes), as described in subsections II.1-5, can contribute to determining the outcomes of agonistic interactions and structure dominance hierarchies in animal groups. Factors are illustrated as partially separate to highlight that most studies to date have considered these independently when attempting to identify factors that determine the outcomes of dominance interactions (open oval) and how these integrate to determine individuals' positions in the dominance hierarchy (open box). The colours of filled shapes each refer to one of subsections II.1-5.

(6) What determines the importance of a particular factor to an interaction outcome?

Variation in the importance of particular factors exists among species. For example, in the nepotistic societies of spotted hyenas and primates, maternal support is a primary determinant of interaction outcomes and thus dominance relationships (Holekamp & Smale, 1991). In contrast, in species with no extended parent-offspring associations, parental support in agonistic interactions is not possible and therefore not important. Given that such differences in the presence/absence of factors across species are unlikely to change in the timescale relevant to dominance hierarchies, variation among species in the importance of different factors is likely to be relatively static.

Whether a factor affects the outcome of a particular interaction (i.e. within a species) depends on the dyadic *difference* in that factor between two contesting individuals (Beacham, 1988). For example, the correlation between hierarchy position and mass in groups of domestic pigs were stronger when there was greater variation in mass – suggesting that body size (an intrinsic attribute) is more influential in determining interaction outcomes when greater variation in body size existed (McBride, James, & Hodgens, 1964; Meese & Ewbank, 1973). This is easily illustrated by winner-loser effects: if an individual is in a loser state, then winner-loser effects will play a much larger role in determining the interaction outcome if its competitor is in a winner state than if the competitor is also in a loser state. Similarly, whether third-party support affects interaction outcomes necessarily depends on first the presence of, and second the intervention by, third-party individuals (Kawai, 1958; Scott, 1980). Thus, for a given agonistic interaction, the dyadic difference across all possible factors (Fig. 1) relevant to that species will predict which individual wins, while at the group and species level factors with greater inter-individual variation within groups will have greater relevance (McBride *et al.*, 1964).

III. Dynamics of interaction outcomes and their determinants

State-behaviour feedback loops have been widely explored in behavioural ecology (Sih *et al.*, 2015). For example, cannibalism in salamanders *Hynobius retardatus* drives increased structural size, which in turn increases rates of cannibalism, leading to positive feedback between behaviour (cannibalism) and state (structural size) (Kishida *et al.*, 2011). The formation and maintenance of dominance hierarchies also represents a case of state-behaviour feedbacks, although to date feedbacks in the context of dominance have primarily been considered in the context of winner-loser effects (but see Hobson & DeDeo, 2015). There is also a paucity of studies integrating multiple, interconnected factors that affect interaction outcomes. In many cases this is likely due to the practical challenges associated with studying multiple factors at once. However, the factors determining dominance interaction outcomes have to date not only been considered independently, but have also mostly been treated as mutually exclusive and therefore competing (e.g. winner-loser effects vs. intrinsic attributes, Beaugrand, *et al.*, 1996; Chase *et al.*, 2002; Hsu *et al.*, 2006) as opposed to forming part of a feedback dynamic in which factors can affect one-another via interaction outcomes. In this section, we outline some of the numerous potential feedback loops that can link interaction outcomes back to the factors that determine them, thereby highlighting how different factors can be highly interconnected.

(1) Feedbacks to intrinsic attributes

Interaction winners often gain priority access to resources, which can in turn affect intrinsic attributes such as size, muscle mass or condition. Although this is not a novel idea (Würdinger, 1975; Black & Owen, 1987), such feedback from interaction outcomes to the factors that determine them is often overlooked. Feedback from interaction outcomes to intrinsic attributes are easily illustrated in contests regarding food, where a winner consumes and assimilates the contested food item, thereby affecting its intrinsic attributes (e.g. weight) in subsequent contests. In groups of domestic pigs *Sus scrofa domesticus* that were formed *de novo* hierarchy position did not relate to body mass (Meese & Ewbank, 1973), yet individuals' positions in the dominance hierarchy was correlated with mass in groups that were well-established (McBride *et al.*, 1964). These results suggest that, by influencing access to food, interaction outcomes over time affect intrinsic attributes.

Feedback from interaction outcomes to intrinsic attributes does, however, not only occur via access to food. Consider a species such as the long-tailed tit *Augithalus caudatus* in which overnight mass losses are considerable (Hatchwell *et al.*, 2009) and group members compete for optimal roosting spots (McGowan *et al.*, 2006). Those individuals in best condition should (all else being equal) gain access to more optimal roosting positions, thereby losing the least mass overnight and subsequently being able to reclaim the optimal roosting spots the following night. Dominant Japanese macaques *Macaca fuscata* also occupy more central positions in huddles (Ishizuka, 2021), which likely confer thermoregulatory benefits allowing these individuals to preserve energy that can then be reinvested in maintaining dominance. More extreme examples of such feedbacks exist where individuals of differing social status differ in growth rate irrespective of access to food. For example, in meerkats *Suricata suricatta*, subordinates respond to experimentally increased growth rates of same-sex peers by increasing their own food intake and growth rates. Upon achieving a dominant breeding position, meerkats then show another period of enhanced growth, the magnitude of which depends on the size difference to the next largest same-sex subordinate (Huchard *et al.*, 2016). Similar processes also take place in some fish species, whereby individuals regulate growth rates to maintain size differences with dominant individuals to avoid conflict (Buston, 2003; Wong *et al.*, 2008). Therefore, via processes such as strategic growth or asymmetrical access to resources such as food or roosting sites, the outcomes of dominance interactions have the potential to shape individuals' intrinsic attributes, which can, in turn, shape future interactions.

(2) Feedbacks to resource value

To a focal individual, the outcome of a previous interaction can—by modulating access to a resource—affect the value of a similar resource in a subsequent interaction. For example, if an individual does not gain access to a food item in agonistic interaction i, it will value a similar food item in interaction i+1 higher than if it had successfully acquired the previous food item (as in section III.2), thereby increasing its investment in interaction i+1. Such positive feedback loops may exist between interaction outcomes and resource-value asymmetries in a range of contexts. One such context is owner-intruder dynamics, because individuals can be expected to value a resource they 'own', such as a burrow or territory, more highly with increasing ownership time (Smith & Parker, 1976). For example, in the case of contested territories, winning an interaction—and thus territory—increases the territory value to the winner, which will generate positive feedback between interaction outcomes and resource value, thereby stabilising outcomes of future dominance interactions. Feedbacks from interaction outcomes to factors can act in opposing directions. For example, when an individual wins a contest for a food item, in a subsequent contest an identical food item will likely be valued lower leading to reduced contest investment, which therefore represents negative feedback to resource-value asymmetry. However, the feedback to winner-loser state will be positive, as winning the initial interaction will place the individual in a winner state. How these different feedback loops operate together remains unknown and would warrant theoretical and empirical study.

(3) Feedback to winner-loser effects

The clearest case of interaction outcomes feeding back to the factors determining them is that of winner-loser effects. As described in section II.3, these effects are defined by the outcome of a previous interaction dictating an individual's winner or loser state in a subsequent interaction, which influences the probability of that individual winning the latter interaction (Chase *et al.*, 2002). As multiple feedback loops act simultaneously, feedback to winner-loser effects has the potential to amplify the results of initial interactions, in which the outcomes can be determined by other factors (e.g. size or third-party support), thereby setting individuals on a path to winning or losing. Ultimately, as winners are more likely to keep winning, and losers to keep losing, this is a case of positive feedback which may stabilise dominance hierarchies (Rutte *et al.*, 2006).

(4) Feedback to dyadic interaction-outcome history

While winner-loser effects can influence subsequent interaction outcomes with any interaction partner, in the case of dyadic interaction-outcome history, only previous interaction outcomes *within the focal dyad* are of importance. In contrast to winner-loser effects, previous dyadic interaction outcomes can affect subsequent interactions in the long-term, though it is unlikely that all past interactions are weighted equally. For example, in contesting green anoles *Anolis carolinensis*, losers reduced aggression when re-paired with the same opponent after three days but not after ten days, which wasn't the case for unfamiliar individuals (Forster *et al.*, 2005). This suggests that more recent interaction outcomes have more influence on future interaction outcomes within the dyad, likely because the reliability of information on the opponent decays. Similarly, in Rainbow Trout *Oncorhynchus mykiss,* after an initial interaction, aggression between familiar individuals increased with time spent separated but not between unfamiliar individuals (Johnsson, 1997). Regardless of previous interactions having a diminishing influence with time, dyadic interaction outcome history represents a potential positive feedback loop that causes interaction outcomes to follow the pattern of previous interaction outcomes, stabilising dominance relationships.

The feedback to dyadic interaction-outcome history may have consequences for other factors and feedback loops. For example, as with feedback to winner-loser effects, this loop is likely to reinforce the effects of other factors, such as intrinsic attributes, on interaction outcomes. Feedback to dyadic interaction-outcome history should thereby amplify dyadic differences in these other factors, which increases the probability that winners to carry on winning. Additionally, this feedback should therefore also reduce the importance of other factors to interaction outcomes over time (e.g. Chaine *et al.*, 2018). For example, using information from previous dyadic interaction outcomes is a more effective strategy of navigating the social landscape than cruder winner-loser effects (Johnsson, 1997). Accordingly, studies of dominance interactions at the onset of group formation, or after a major disturbance to a group, could conclude certain factors to be more or less important than studies of groups with stabilised hierarchies, as interaction history increases in importance over time.

(5) Feedbacks to social support

An individual's position in the dominance hierarchy, which is determined by previous interaction outcomes, often modulates the degree of social support it receives, although current evidence comes primarily from hyenas and primates. In spotted hyenas, individuals intervening in ongoing agonistic interactions typically support the individual higher in the hierarchy (Smith *et al.*, 2010). Third-party individuals in vervet monkeys *Chlorocebus pygerythrus* consistently support the more dominant individual when joining (dyadic) agonistic interactions (Borgeaud & Bshary, 2015). In female savannah baboons *Papio cynocephalus*, individuals predominantly provide support to the individual positioned higher in the hierarchy (Silk, Alberts, & Altmann, 2004). Thus, social support can act as a positive feedback loop, like interaction outcome-history, to enhance effects of factors that place individuals higher in the dominance hierarchy, ultimately stabilising dominance relationships (as suggested by Silk *et al.*, 2004).

(6) A dynamic dominance framework

Combining the factors and feedback loops described in sections II and III, respectively, produces a conceptual framework that outlines how, over time, interaction outcomes and the factors that determine them can interact (Fig. 2). While it is possible that the factors determining interaction outcomes, such as intrinsic attributes and resource value asymmetries, are fundamentally linked rather than through the outcomes of agonistic interactions, we suggest that the study of dominance will benefit from regarding these factors as parts of a dynamic and highly inter-connected process.

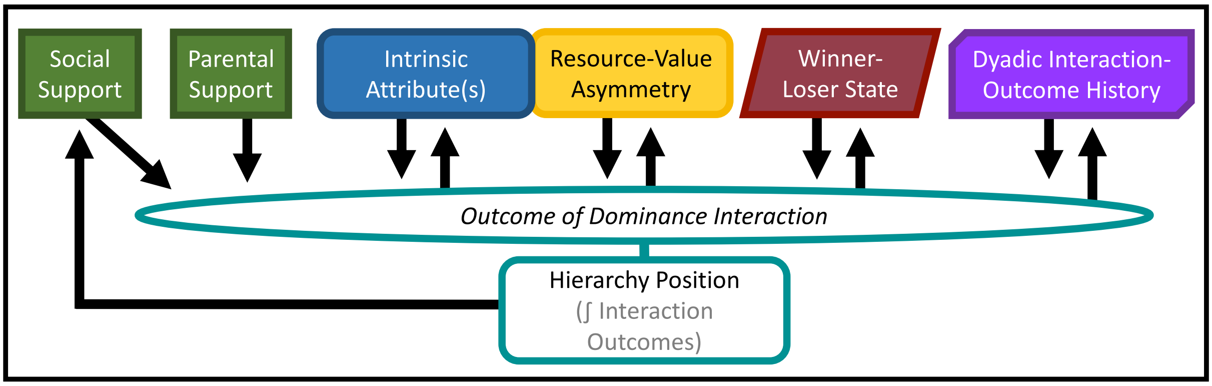

Fig. 2. Outcomes of dominance interactions can feed back onto the factors that determine outcomes of future dominance interactions. By combining sections II and III from the main text, we can create a conceptual dominance framework that reveals numerous potential feedback loops between interaction outcomes and the factors that determine them. These feedbacks, which can cross into different factors, demonstrate that factors determining outcomes of dominance interactions are unlikely to operate independently or in isolation of others. All colours in the figure correspond to those in Fig. 1.

In our framework, subsections II.1-5 and III.1-5 can each be thought of as a testable hypothesis (illustrated as arrows in Fig. 2) that has received varying levels of empirical support. For example, the arrow from social support to the outcome of dominance interactions represents the hypothesis that social support influences interaction outcomes, which Vullioud et al. (2019) provide support for in spotted hyenas. Similarly, the arrow from winner-loser state to outcome of dominance interaction illustrates the hypothesis that an individual’s winner or loser state influences a subsequent interaction outcome, for which evidence has been found in species ranging from fruit flies *Drosophila melanogaster* (Trannoy *et al.*, 2016) to primates (Franz *et al.*, 2015). While some pathways we discuss will be of little importance in particular taxa, we aimed to provide an account of the main pathways that are likely to have importance across a range of species, whilst retaining a level of conciseness that provides practicality.

IV. Parental effects on the determinants of interaction outcomes in offspring

An individual’s dominance status and the factors determining interaction outcomes are not only highly interlinked, but will often also influence factors important to its offspring’s dominance (Bernardo, 1996; Mousseau & Fox, 1998). A range of pre-natal and post-natal effects—such as propagule size, timing of breeding or the quality of parental care—can allow parents to influence the factors that determine their offspring’s interaction outcomes. However, despite being integral to shaping dominance in animal societies, the mechanisms underlying parental effects are rarely considered (but see Holekamp & Smale, 1991; Weiß, Kotrschal, & Foerster, 2011). Below, we describe routes by which parents can influence offspring success in winning dominance interactions and illustrate how feed-forward mechanisms can connect to the feedback loops discussed in section III (Fig. 3).

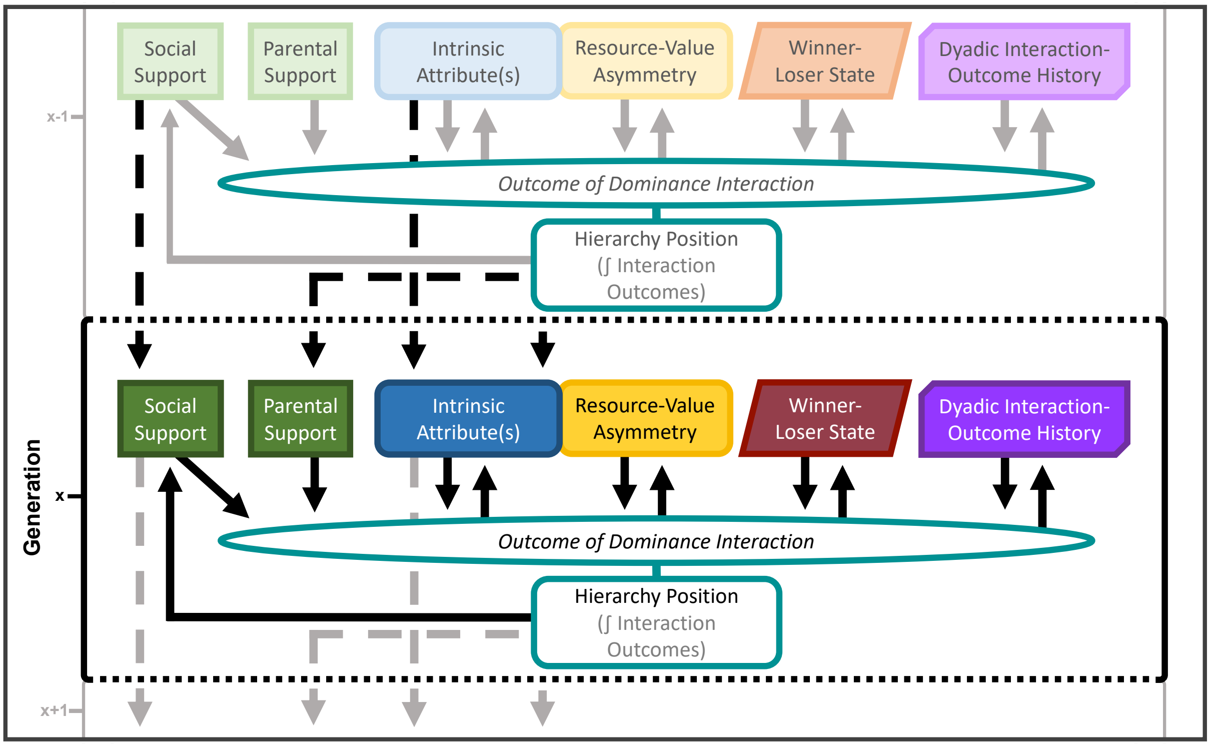

Fig. 3. Integrating transgenerational (feed-forward) mechanisms with factors determining interaction outcomes and their feedbacks. Interaction outcomes and the factors that determine them (Fig. 2) which operate in a previous generation (x-1) can affect interaction outcomes in a focal generation (x). Potentially important parental effects to generation x are coloured in black, while those important to the previous or subsequent generations are coloured in grey. Within-generation influences are denoted by solid arrows, while parental effects are represented by dashed arrows. Note that in most species, generations are overlapping and not distinct as may be inferred from this diagram. The factors affecting interaction outcomes in a focal generation are coloured as in Fig. 1 & 2.

(1) Parental effects on offspring intrinsic attributes

Parents can influence offspring intrinsic attributes via multiple routes. For example, parents universally affect the intrinsic attributes of offspring via genetic inheritance (Wolf & Wade, 2009), which encompasses both physical (e.g. size, Wilson, Kruuk, & Coltman, 2005) and behavioural (e.g. aggression, see Drews, 1993) traits. However, of greater interest to the study of dominance are the many potential non-genetic feed-forward mechanisms by which offspring can benefit from parents (Mousseau & Fox, 1998; Wolf & Wade, 2009). A common pathway could be via early-life growth rates, which can have considerable consequences for dominance acquisition in later life (e.g. female meerkats *Suricata suricatta* that grow faster until nutritional independence are more likely to become dominant, English *et al.*, 2013). Early-life growth rates can be affected by both pre- and post-natal parental investment as well as parental nepotism. A meta-analysis by Krist (2011) found that female birds which invest in larger eggs produce chicks that are larger and grow faster, demonstrating that pre-natal investment influences early-life growth rates. An example of post-natal effects is seen in house wrens *Troglodytes aedon* where parents that deliver more food to the nest raise heavier chicks (Bowers *et al.*, 2014). Experimental evidence in white-tailed deer *Odocoileus virginianus* confirms such direct links between parental condition and offspring development, with growth rates of fawns from food-restricted mothers being reduced by 26% (Therrien *et al.*, 2008). In species with parent-offspring associations, dominant parents can also nepotistically allow offspring access to food resources. For example, cubs of dominant spotted hyena mothers gain considerable advantages in accessing food in competitive feeding situations (Frank, 1986). In carrion crows *Corvus corone corone* nepotistic tolerance at experimental food sources allows the offspring of dominant breeding males to spend more time feeding than immigrants who would otherwise be dominant to the offspring (Chiarati *et al.*, 2011). Parental support by dominant Bewick's swan pairs similarly reduces offspring feeding competition, which may allow enhanced offspring growth rates and thus size (Scott, 1980). The offspring of dominant meerkat mothers have been shown to grow faster while reliant on helper care (English *et al.*, 2014), suggesting that the effect of parental dominance on offspring intrinsic attributes could occur via third-party individuals. This could occur if the offspring of more dominant parents receive more care or food-provisioning from helpers. Parental effects could also come from differences in the timing of reproduction, for example if the offspring of dominant individuals emerge earlier and are larger than their cohort mates (English *et al.*, 2014). Accordingly, because access to food resources—especially in early life—can have long-term consequences for an individual's intrinsic attributes (Richner, 1992), parental investment and nepotism can shape offspring intrinsic attributes with likely downstream effects for the ability of offspring to win agonistic interactions in later life.

Parental effects on offspring intrinsic attributes, and subsequent establishment of dominance, can also come from a number of pathways not directly related to growth rates. For example, mothers can vary hormone levels to which developing young are exposed (Mousseau & Fox, 1998), with exposure to higher androgen levels known to relate to higher rates of aggression or dominance status in mammals (Dloniak, French, & Holekamp, 2006) and birds (Schwabl, 1993). Moreover, the timing of birth or hatching is an almost ubiquitous maternal effect that can influence offspring growth rates, for example via competitive ability in early life, and is often itself influenced by parental intrinsic attributes (e.g. condition, Bêty, Gauthier, & Giroux, 2003). For example, in bison *Bison bison*, earlier-born calves grow faster, reach a larger size, and attain a higher position in the dominance hierarchy than later-born cohort mates (Green & Rothstein, 1993). Taken together, the evidence presented here suggests that parents can influence the factors that determine interaction outcomes in offspring through diverse mechanisms, including investment in offspring, timing of reproduction and the programming of offspring development.

(2) Parental effects on offspring third-party support

When offspring engage in dominance interactions, the quality of support they receive from their parents is unlikely to be equal among all individuals. For example, in spotted hyenas, dominant mothers provide both more effective and more frequent support to their offspring (Engh *et al.*, 2000) – despite dominance not being driven by physical size (Vullioud *et al.*, 2019). Similar patterns have been described in primates (Maestripieri, 2018) and birds (Bewick's swans, Scott, 1980). Thus, the degree of parental dominance often influences the quality of parental support individuals receive and, thereby, offspring interaction outcomes and resulting hierarchy position.

In addition to parental support, the offspring of adults higher in the hierarchy could receive greater third-party support from non-parents, here termed 'social support' (see section II.5b). It has been suggested that offspring in group-living species may inherit their parents' social associations (Goldenberg, Douglas-Hamilton, and Wittemyer 2016; Ilany and Akçay 2016; de Waal 1996; but see

Ogino, Maldonado-Chaparro, and Farine, 2021); recent work in spotted hyenas has demonstrated a strong correlation between parent and offspring social associations that persists for up to six years (Ilany, Holekamp, & Akçay, 2020), demonstrating the potential for offspring to inherit coalition partners. Such social inheritance of parental associations could occur simply via passive space-use processes – where offspring remain with their parents who tend to move in proximity to their affiliates, resulting in offspring and parental affiliates (or their offspring) forming associations (Ilany & Akçay, 2016). Thus, transgenerationally-linked social associations can have important consequences for the quality and quantity of social support individuals receive.

V. Methods for studying dominance and its determinants

(1) Dynamics of hierarchy position and the factors determining interaction-outcomes

In a review of the study of feedbacks in the context of animal personality, Sih et al. (2015) outlined how researchers may investigate the links between an individual's behaviour and its state, which has helpful parallels to the feedbacks discussed above. When considering feedbacks in the context of dominance interactions, 'state' can be considered analogous to the factors outlined in section II (e.g. intrinsic attributes or winner-loser state), while 'behaviour' corresponds to outcomes of dominance interactions (i.e. win/loss). We thus suggest a similar approach should be applicable for understanding the feedback loop between interaction outcomes and a particular factor. For example, experimental manipulation of a factor important to determining interaction outcomes, combined with tracking the effects on hierarchy dynamics in the long term, will allow researchers to separate positive from negative feedback loops.

Methodological developments in the field of dominance have also provided increasingly advanced analytical tools crucial for studying hierarchy dynamics. Elo scores, introduced to behavioural ecology two decades ago, provided a solid platform for such developments due to an individual's score at any particular point, relative to that of conspecifics, reflecting an individual's probability of winning the next dominance interaction (Albers & de Vries, 2001). With the publication of user-friendly R functions (Neumann *et al.*, 2011; Sánchez-Tójar, Schroeder, & Farine, 2018) and methods to formally track how individual ranks change through time (Strauss & Holekamp, 2019b), Elo scores have become increasingly popular among behavioural ecologists. Several features of Elo scores could be useful in the study of feedbacks. For example, the contribution of different interaction types to Elo scores can be modelled by modifying the weighting of each interaction type when updating scores (via the parameter *K,* Newton-Fisher, 2017; see also Franz *et al.*, 2015). Furthermore, the importance of temporal ordering of interactions can be quantified by comparing the observed hierarchy to permutations in which the ordering of interactions is randomised (Sánchez-Tójar *et al.*, 2018). Finally, Elo scores explicitly include information on how reversals (where a subordinate wins) violate expectations given the differences in scores between actors, thereby providing a tool to identify whether different drivers predict highly unexpected outcomes. While there are a number of promising tools for the study of feedbacks as they link interactions and their outcomes over time, there remains much scope for more development of integrative approaches focused on extracting potential feedback mechanisms (e.g. as suggested by Sih *et al.*, 2015) with those that have been developed for studying hierarchy dynamics.

While the study of single feedback loops in isolation will allow us to tease apart feedback mechanisms and the direction of their effects, multiple feedback loops likely act simultaneously in most animal groups. We suggest that these many routes for feedback from interaction outcomes to the factors that determine them, as described in section III, represent a complex system. These systems are difficult to define, but typically have features such as feedbacks, hierarchical organisation, non-linearity, robustness and a lack of central control (Ladyman, Lambert, & Wiesner, 2013). Importantly, complex systems involve multiple feedback processes that increase or decrease in importance given different conditions. Support for such a perspective comes from evidence that dominance hierarchies that are disturbed can rapidly become chaotic before restabilising in a new state (Strauss & Holekamp, 2019a), highlighting how dominance hierarchies can have highly unstable states interspersed with long periods of stability. Implementing tools and approaches from complex systems sciences, as have been applied in other areas of ecology (e.g. forest ecology, Filotas *et al.*, 2014; social complexity, Hobson *et al.*, 2019; land-water food webs, Sullivan & Manning, 2019; see also Anand *et al.*, 2010) may prove to be a constructive way forward for understanding the mechanisms that underpin hierarchy structure and stability.

(2) Integrating different interaction types

Multi-layer networks provide a framework that allows different types of interactions to be modelled explicitly, rather than simply varying the contribution of different interaction types (Finn *et al.*, 2019). For example, there may be network motifs (patterns of dominance) that play out across different layers (where a layer represents one type of interaction), which could reveal how different interaction types operate together. Such approaches could further reveal whether patterns are consistent across species (Shizuka & McDonald, 2015) or whether individuals' traits (e.g. state, prior attributes) predict the patterns of interactions they express or receive. Alternatively, multi-layered network analysis can help to decide whether to pool or separate interaction types for further analyses based on whether interaction types are functionally different (van der Marel *et al.*, 2021). Integrating multi-layered networks with dynamic network methods (Hobson, Avery, & Wright, 2013; Farine, 2018) further makes it possible to test whether certain types of interactions consistently precede others, or whether the outcomes of previous interactions predict the intensity, type, or outcomes of following interactions (e.g. via winner-loser effects, or to identify changes in resource value). As well as constructing interaction networks that change over time, it is also possible to extract networks across different contexts, such as interactions that take place over food versus in competition for mates. These can then be formally compared to test whether individuals express different strategies under different conditions. Thus, continued developments in network-based tools provide promising avenues for identifying dynamics and feedbacks in dominance interactions.

(3) Experimental approaches

A major challenge for understanding feedback and feed-forward mechanisms underlying dominance outcomes is that they require studying social behaviours of animals over long periods of time. Further, in natural populations, there may be multiple potential pathways that are difficult to disentangle. For example, offspring dominance interaction outcomes in spotted hyenas may be related to parental hierarchy position due to one (or more) of the following: genetic inheritance of predisposing intrinsic attributes, prenatal exposure to maternal hormones or maternal support in agonistic interactions (see East *et al.*, 2009). Disentangling such proximate mechanisms poses a methodological challenge in natural systems, which therefore often rely on correlational analyses of rare cases of natural adoptions (e.g. East *et al.*, 2009; but see Dantzer *et al.*, 2017).

Understanding dominance will require experimental manipulations. However, conducting manipulations might require broadening research to species in which it is feasible to experimentally tease apart potential mechanisms. One such taxon are birds, which have many advantages. For example, eggs or offspring are easily cross-fostered, allowing experimental manipulation of pre- and post-natal environments (Winney *et al.*, 2015). There is also evidence that some birds live in societies similar in complexity to those of social mammals (e.g. vulturine guineafowl, Papageorgiou *et al.*, 2019), with many others living in stable social groups (e.g. southern pied babblers *Turdoides bicolor,* Ridley, 2016), and such groups have prominent dominance hierarchies. Thus, developmental drivers of dominance outcomes in later life can be experimentally quantified, for example through brood size manipulations, cross-fostering, or by manipulating the timing of hatching. Other taxa, such as clonal fish, also provide ideal experimental systems because all individuals start with the same genetic template (Laskowski *et al.*, 2016). The manipulation of the factors discussed in section II on an individual level will also be facilitated by the development and availability of novel technologies. ‘Smart feeders’ for example can selectively open depending on the individual(s) present (Ibarra *et al.*, 2015; Firth, Sheldon, & Farine, 2016; Bridge *et al.*, 2019) and could be used to not only allow/prevent particular individuals to feed, but also vary the nutritional value of food items individuals have access to. Studies have demonstrated that changing the social structure can alter population processes, such as information transmission (Firth *et al.*, 2016). By implementing such technologies, it is possible to manipulate factors such as intrinsic attributes (e.g. via differential food access and thus growth and size) or resource-value asymmetries (e.g. affect the value of a given area/territory by differential feeder access). Similar experimental innovations have been carried out in homing pigeons, where researchers attached artificial weights to the backs of ~50% of group members, causing increased dominance scores in mass-loaded individuals and the temporary disruption of the established hierarchy (Portugal *et al.*, 2020). Experimental manipulations will play a major role in eventually unpacking the complex feedback and feed-forward dynamics that underpin dominance outcomes.

VI. Outstanding questions

(1) Do feedback loops generate variation in factors that determine interaction outcomes?

Stable differences among individuals may emerge from minimal initial variation. One such factor is winner-loser effects, which are by definition absent in individuals prior to their first agonistic interaction yet emerge over time as individuals have repeated interactions causing a divergence in states: as winners gain a ‘winner state’ and losers gain a ‘loser state’. Further, given that interaction outcomes are generally predicted by dyadic differences in factors, as opposed to their absolute values, it is likely that at any given point in time different groups differ in the importance of each factor based on how much inter-individual variation exists and how different pathways increase or decrease variation (through positive/negative feedbacks). Thus, understanding how interaction outcomes feed back to the factors determining them is likely to be critical for understanding how variation in dominance, and thereby dominance hierarchies, emerges among individuals.

(2) How do interaction outcomes combine to determine hierarchy position?

A major outstanding question is exactly how interaction outcomes contribute to the position of individuals in a dominance hierarchy. Analytical dominance ranks or scores are typically constructed or calculated from a variety of agonistic interactions that are known to reliably demonstrate dominance relationships in the focal species (Levy *et al.*, 2020). Usually, different types of agonistic interactions receive the same weighting (i.e. importance) when inferring analytical dominance hierarchies (Papageorgiou & Farine, 2020), yet it is likely that interaction types differ in their functional importance to dominance relationships in animal groups (van der Marel *et al.*, 2021). For example, more intense or escalated aggressive interactions can increase the impact of wins and losses on future wins and losses (Franz *et al.*, 2015) and may thus be weighted more heavily (Newton-Fisher, 2017). In addition, it is easy to conceive a scenario in which outcomes of agonistic interactions that oppose the dyadic interaction history due to resource-value asymmetries could, functionally, have minimal impact on the long-term position of individuals in the hierarchy. For example, individual A is dominant to individual B and typically wins all interactions, but B wins interaction i against A due to valuing a contested resource much more highly. If the two individuals value a resource equally and compete for it in interaction i+1, providing the resource obtained by B in interaction i does not substantially influence B's ability to win interactions more generally (e.g. through growth), A can be expected to win interaction i+1. If this is indeed the case, it raises the question whether interaction outcomes that are due to resource-value asymmetries can be considered as 'dominance interactions' at all. Ultimately, such variation in weighting of interaction outcomes could result in mismatches between the real dominance hierarchy and the inferred hierarchy. Understanding how different factors influence the outcomes of dominance interactions and their feedback loops will be important to unravel how these processes combine to determine individuals' hierarchy positions.

(3) Do stochastic interaction outcomes affect individuals' hierarchy positions?

One key question is to what extent stochasticity influences the positions of individuals in their dominance hierarchy. As positive feedback loops act to stabilise interaction outcomes over time, in species where the more influential feedback loops are positive, we should expect a stochastic interaction outcome to be amplified and thus have a greater effect on individuals' hierarchy positions. When positive feedback loops are very strong (substantially increasing the probability of interactions to follow the interaction history), then the frequency of stochastic interaction outcomes is likely to be much lower. Thus, the more influential positive feedback loops are in a given system, the less frequent but more important individual stochastic interaction outcomes may be. In any case, such stochastic effects may be most important when individuals join groups (i.e. in early life or after immigration) – when some factors important to interaction outcomes, e.g. dyadic interaction-outcome history, are yet to be established.

(4) Do feedback loops act as self-organising mechanisms and generate linear hierarchies?

The feedback processes we have described likely represent forms of 'self-organisation', in which hierarchies are "produced by the dynamics of social interactions" (Chase *et al.*, 2002), and may help to explain repeated observations of linear hierarchies. There is remarkable conservation of hierarchy structure across diverse taxa, with more transitive triads relative to cyclical triads than expected by chance (McDonald & Shizuka, 2012). Previous studies of hierarchy structure have often attempted to explain this pattern via the social dynamics hypothesis—positing that hierarchies emerge solely from winner-loser effects, and are thus 'self-organising'—but winner-loser alone effects do not explain all variation observed in hierarchy structure (Lindquist & Chase, 2009). We propose that the many routes for positive feedback from interaction outcomes to their determinants, described above, also represent forms of 'self-organisation' as per the above definition. If indeed the case, the term 'self-organisation' thus not only applies to winner-loser effects but also other, interconnected factors that determine interaction outcomes and ultimately dominance.

(5) Does feedback exist across generations?

Parental effects can influence offspring dominance, as described above, but whether offspring can also influence parental dominance remains unexplored. In species with overlapping generations and extended periods of parent-offspring associations, adult offspring co-exist with their parents in the same social group for extended periods of time, as in many cooperative breeders (Stacey & Koenig, 1990; Koenig & Dickinson, 2016). In such species, offspring could influence the factors that determine the interaction outcomes of their parents with non-relatives, e.g. by lending social support. Few studies have investigated whether such effects exist. However, spotted hyena cubs have been found to act nepotistically towards their sires relative to control males (Van Horn, Wahaj, & Holekamp, 2004). Thus, in addition to transgenerational feed-forward mechanisms, there may also exist transgenerational feedback loops that link a focal generation back to its parental generation.

VI. Conclusions

(1) Multiple factors can simultaneously influence the outcomes of dominance interactions in animal groups including intrinsic attributes, resource-value asymmetry, winner-loser effects, dyadic interaction-outcome history, parental support and social support. The importance of each factor in determining interaction outcomes i) varies between species and ii) increases with inter-individual variation in the factor of interest.

(2) Here, we emphasize that the outcomes of dominance interactions also impact the factors that determine them, meaning that interaction outcomes and these factors are highly interconnected via feedback loops. These feedbacks may operate through multiple mechanisms, including by mediating access to resources, determining winner-loser state, influencing the social-support choices of conspecifics, and shaping individuals’ dyadic interaction history. It is therefore crucial that researchers are conscious of these feedback loops when ascribing causality to dominance, as factors that have previously been described as a cause of dominance may in fact be a consequence.

We describe a conceptual framework and illustrate what are likely to be the most common feedback loops that make social dominance and its determinants a dynamic system.

(3) Feedback loops between interaction outcomes and the factors that determine them in parents can, via parental effects, feed forward to a subsequent generation and affect the outcomes of offspring dominance interactions. Such effects can occur via many routes, including investment in offspring, altering the developmental environment of offspring or by intervening in the agonistic interactions of offspring. We therefore embed the conceptual framework of interaction outcomes and the factors that determine them in a transgenerational approach that considers the multiple routes by which parents may influence offspring social dominance.

(4) We suggest that the manipulation of a particular factor important to determining interaction outcomes may, in combination with the tracking of hierarchy dynamics, allow researchers to distinguish positive from negative feedback loops. Additionally, we encourage the study of dominance in species in which parental effects are easily manipulated, which will allow the causal investigation of mechanisms underpinning parental dominance effects. While recent analytical developments facilitate the study of hierarchy dynamics, novel approaches are likely needed to overcome the analytical (and empirical) challenges of studying multiple feedback loops acting simultaneously. We suggest that approaches from complex systems sciences may provide a solution to studying the effects of these feedback loops on hierarchy dynamics.

(5) We highlight several important research gaps. Research of parental effects on offspring dominance should be undertaken in a broader range of taxa and study mechanisms other than matrilineal support, such as the parental timing of reproduction. Further, more research—both empirical and theoretic—is needed to understand how interaction outcomes combine to determine hierarchy position, and therefore hierarchy stability. By stimulating more studies to explicitly consider the feedback loops and feed-forward mechanisms between interaction outcomes and the factors that determine them, we hope that our framework will lead to a better understanding of the processes underpinning social dominance in animal groups.

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