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

Authors

Tobit Dehnen[1,2,3,*], Josh J. Arbon[1], Damien R. Farine[2,3,4,a] and Neeltje J. Boogert[1,a]

[1] Centre for Ecology and Conservation, University of Exeter, Penryn Campus, Treliever Road, Penryn TR10 9FE, UK

[2] Department of Collective Behavior, Max Planck Institute of Animal Behavior, Universitätsstraße 10, 78464 Konstanz, Germany

[3] Department of Evolutionary Biology and Environmental Studies, University of Zurich, Winterthurerstrasse 190, 8057 Zürich, Switzerland

[4] Centre for the Advanced Study of Collective Behaviour, University of Konstanz, Universitätsstraße 10, 78464 Konstanz, Germany

[a] Authors contributed equally to this work

* Address for correspondence: (E-mail: td430@exeter.ac.uk; Tel: +44 1326 255986)

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 a variety of factors are likely important to interaction outcomes, and thereby individuals' dominance hierarchies positions, in diverse species. We propose that such factors are unlikely to independently determine dominance outcomes, but rather form part of 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 that illustrates the multitude of potential routes through which such feedbacks can occur, and how the factors that determine outcomes of dominance interactions are highly intertwined and thus rarely act independently of one-another. Further, we generalise our framework to include multi-generational feed-forward mechanisms: how interaction outcomes in one generation can influence the factors determining interaction outcomes in the next generation 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: how feedbacks generate variation in the factors discussed, and how this might be studied experimentally; how the relative importance of different feedback mechanisms varies across timescales; the role of social structure in modulating the effect of feedbacks on hierarchy structure and stability; and the routes of parental influence on the dominance status of offspring. Ultimately, by considering dominance interactions as part of a dynamic feedback 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 often leading to aggressive encounters among group-members (Ward & Webster, 2016). Individuals typically differ in their tendency to win such aggressive interactions, resulting in some individuals becoming 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 (McDonald & Shizuka, 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) and mating opportunities (Ellis, 1995); therefore, social dominance has 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 wide-ranging 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 factors hypothesised to 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 intrinsic attributes (Chase *et al.*, 2002), resource-value asymmetries (Smith & Parker, 1976), winner-loser effects (Hsu *et al.*, 2006), dyadic interaction-outcome history (Chaine *et al.*, 2018) and third-party support (Schülke *et al.*, 2010). However, there is a distinct lack of integration between different approaches to dominance, with particular factors central to some approaches yet absent in others. For example, resource value is central to game theory but generally absent in studies of hierarchy structure (Parker, 1974; Maynard Smith & Parker, 1976; Chase *et al.*, 2002). Accordingly, the factors affecting interaction outcomes are often studied separately (but see Lerena, Antunes, & Taborsky, 2021) and have been implied to act largely independently from one another (Chase *et al.*, 2002; Holekamp & Strauss, 2016). However, it is likely that a combination of multiple factors determines the outcome of a particular interaction in most species.

Drivers of interaction outcomes are not only unlikely to act in isolation but may, importantly, also interact with one another via feedback loops—mirroring state-behaviour feedback in other areas of ecology (Sih *et al.*, 2015)—and thus change over time. 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 is likely to 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 that integrates the many potential factors involved in structuring dominance relationships remains absent (Holekamp & Strauss, 2016). Here, we aim to unify different approaches and provide a more complete framework of the processes that shape and maintain dominance relationships in natural populations. With this, we hope to stimulate future research that explicitly considers feedback loops and to encourage broader considerations of how dominance may emerge and be maintained. Doing so will ultimately provide a clearer view of the causes and consequences of dominance in animal groups across generations.

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 and *any* dominance interactions occur among its members (e.g. in experimental studies, Chase *et al.*, 2002). 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 are static, which is unlikely to be the case due to inevitable developmental changes as well as changes in resource access (Polo & Bautista, 2002), improved fighting skill or practice (Hsu *et al.*, 2006; Sih *et al.*, 2015) injuries (Clutton-Brock *et al.*, 1979) or changes in badges of status (Dey, Dale, & Quinn, 2014). Additionally, 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 and, to avoid such problems with the term ‘prior attributes’, we suggest the use of ‘intrinsic attributes’ (Beacham, 2003; Vullioud *et al.*, 2019) instead and refer to them as such here.

Single intrinsic attributes rarely affect dominance interactions in isolation from other traits. Typically, researchers use a measures of size, mass, length or height as a proxy for *all* intrinsic attributes that affect interaction outcomes, which is then related 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; Arnott & Elwood, 2009; 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). Such 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). Accordingly, causality in a positive relationship between an intrinsic attribute and dominance (for examples, see Table 2 in Hsu *et al.*, 2006)—especially in established social groups in that have long-standing dominance hierarchies and individuals at different developmental stages—should not be assumed (Huntingford *et al.*, 1990). Instead, experimental manipulations or staged contests are required to infer causality in a positive relationship between intrinsic attributes and dominance or winning propensity.

(2) Resource-value asymmetry

Game-theoretic approaches have long considered differences in the value of a contested resource between competing individuals to influence contest outcomes (Parker, 1974; Maynard Smith & Parker, 1976), yet such considerations are largely lacking in other studies of social dominance (Holekamp & Strauss, 2016). Nevertheless, many empirical studies have demonstrated that, when two individuals compete for a resource, an asymmetry in individuals' valuations of the resource can influence the outcome of the contest. This is because individuals scale contest investment with perceived resource value and are thus more aggressive, or incur larger costs or greater risks, when competing for resources that are more valuable to them (Enquist & Leimar, 1987; Arnott & Elwood, 2008). For example, in whiptail lizards *Aspidoscelis costata*, males defending larger, and thus more valuable, females are more aggressive (Ancona, Drummond, & Zaldívar-Rae, 2010). Differences in resource value between competing individuals are likely to arise due to individuals' different contexts; when blue-black grassquit *Volatinia jacarina* males contest a food resource, individuals in poorer body condition are more aggressive, and thus more dominant, than those in better condition (Santos, Maia, & Macedo, 2009). Similarly, food-deprived male *Drosophila melanogaster* are more aggressive than fed individuals when competing for a food resource (Edmunds, Wigby, & Perry, 2021). Furthermore, male house crickets *Acheta domesticus* that have no prior access to females, relative to males that do, are more aggressive 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. The individual in possession of the contested commodity usually has more to lose (i.e. a higher resource value) than an intruder, resulting in 'owners' typically winning disproportionately more contests (Maynard Smith & Parker, 1976; Enquist & Leimar, 1987). In male snow skinks *Niveoscincus microlepidotus* competing for burrows, owners win over 70% of contests (Olsson & Shine, 2000); nest-owning European paper wasps *Polistes dominula* are more aggressive than intruders when competing for nests (Injaian & Tibbetts, 2015); and male cichlids *Neolamprologus pulcher* are more aggressive with increasing territory tenure 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 outcome of an interaction. Given the importance of resource value asymmetry in determining contest outcomes in a wide variety of species (e.g. fish, Olsson & Shine, 2000; insects, Injaian & Tibbetts, 2015; and reptiles, O'Connor *et al.*, 2015) and contexts (e.g. when competing for food, Cristol, 1992; Nosil, 2002; mates, Ancona *et al.*, 2010; hosts in which to lay eggs, Mohamad, Monge, & Goubault, 2010; and territories, Bergman, Olofsson, & Wiklund, 2010), it should be given due consideration in studies of dominance, which ultimately study cumulative interaction outcomes.

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 will often be 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, and that this probability is reduced in those that lost their most recent contest (McDonald, Heimstra, & Damkot, 1968; Dugatkin, 1997; Hsu *et al.*, 2006; Rutte, Taborsky, & Brinkhof, 2006). An important feature of winner-loser effects is that they are thought to act regardless of opponent identity (Rutte *et al.*, 2006) and may therefore have pervasive consequences. Additionally, while winner-loser effects act from one interaction to the next, they can ultimately influence individuals' positions in dominance hierarchies, such that winners are positioned higher, and losers lower, in the hierarchy (Dugatkin & Druen, 2004; Laskowski, Wolf, & Bierbach, 2016). Evidence for winner-loser effects 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), but these studies are largely restricted to captive populations. In part, this scarcity of evidence from wild populations is likely due to the challenge of observing continuous interaction outcomes over time. However, intensive observations—over 15,000 dyadic interactions—of savannah baboons, collected over a 15 year period, provide important observational support for winner-loser effects in a wild system (Franz *et al.*, 2015).

An important dimension of winner-loser effects is the temporal persistence of the effect of a single interaction. Winner-loser effects are typically of short duration, lasting for minutes to hours (Hsu *et al.*, 2006), but may persist over longer periods in species in which individuals interact relatively infrequently (e.g. copperhead snakes *Agkistrodon contortrix,* Schuett, 1997; Syrian hamsters *Mesocricetus auratus*, Huhman *et al.*, 2003). Accordingly, the duration of winner-loser effects may, at the species level, be proportional to the individual-level interval between interactions.

While the effect of a single interaction is generally short-lived, individuals may be exposed to *continuous* winning or losing experiences in natural populations where individuals often interact frequently over a short period of time. Such continuous winning or losing can have longer-lasting consequences that extend across periods in which no interactions take place (Trannoy *et al.*, 2016). In Amazon mollies *Poecilia formosa*, for example, continuous winning or losing in early life affects individuals' dominance relationships in later-life, i.e. after 20 weeks, such that losers are at the bottom of triadic dominance hierarchies and winners at the top (Laskowski *et al.*, 2016). Accordingly, given the importance of early-life interactions for individuals' subsequent dominance trajectories (Black & Owen, 1987; Holekamp & Strauss, 2016), long-term consequences of continuous winning or losing could carry over from brood-level dominance into adult dominance relationships, which may persist even if intrinsic attributes change (Black & Owen, 1987).

Winner-loser effects have often been studied in the context of the "social dynamics hypothesis", which posits that hierarchies are 'self-organising' and an orderly (or linear) hierarchy structure arises due to such effects even in the absence of other influences (such as intrinsic attributes, Chase *et al.*, 2002). However, studies of winner-loser effects are often conducted in laboratory settings, where natural variation in other important factors (e.g. size, an intrinsic attribute) can be minimised. Captive studies on winner-loser effects also tend to be of short duration and focus on newly formed groups within a single generation (McDonald *et al.*, 1968; Beacham, 1988; Chase *et al.*, 2002; Dugatkin & Druen, 2004). 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 remains unclear (but see Fuxjager *et al.*, 2009; Franz *et al.*, 2015; Yasuda, Kaida, & Koga, 2020).

(4) Dyadic interaction-outcome history

In species with relatively stable group membership and small group sizes, individuals can often recognise group members individually and pair previous interaction outcomes with the identity of a particular conspecific (Drews, 1993; Hobson, 2020). When such 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;

Newton-Fisher, 2004; Dehnen *et al.*, 2021). The dyadic interaction-outcome history is likely to influence interactions across a wide range of species, even those that use status badges to infer relative dominance. For example, manipulation of status-signalling badges of golden-crowned sparrows *Zonotrichia atricapilla* demonstrate that badges influence the direction of dominance in pairs of strangers, but not between familiar flockmates (Chaine *et al.*, 2018). Similarly, in barnacle geese, body size and weight (i.e. intrinsic attributes) determine dominance relationships among *unfamiliar* goslings, but not between familiar individuals in which the previously established dominance relationship typically prevails (only changing when the difference in size or weight becomes very large; Black & Owen, 1987).

Dyadic interaction-outcome history typically changes the magnitude of the aggression displayed. For example, in pairs of contesting green anoles *Anolis carolinensis*, losers of an initial interaction are significantly less aggressive when repaired with their previous opponent, relative to being paired with an unknown individual (Forster *et al.*, 2005). Similarly, rainbow trout *Oncorhynchus mykiss* (Johnsson, 1997), three-spined sticklebacks *Gasterosteus aculeatus* (Utne-Palm & Hart, 2000), mangrove killifish *Kryptolebias marmoratus* (Edenbrow & Croft, 2012) and hermit crabs *Pagurus middendorffii* (Yasuda *et al.*, 2014) all have lower levels of aggression in contests with familiar individuals relative to unfamiliar individuals. These studies demonstrate that prior interaction outcomes influence the behaviour in, and outcomes of, subsequent dominance interactions within 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 that 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 mechanisms 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 (Holekamp & Smale, 1991). Empirical examples come predominantly from primates (for a review, see Maestripieri, 2018) and spotted hyenas *Crocuta crocuta* (Holekamp & Smale, 1993). However, parental support has also been shown to be important to dominance interactions in birds, including Bewick's swans *Cygnus columbianus bewickii*, in which parental absence greatly 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).

(b) Social support

Third-party support can also be provided by non-parent individuals. Such social 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 common in primates. For example, chacma baboons *Papio ursinus* 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, kin and dominant group members (Fraser & Bugnyar, 2012). Third-party individuals may not need to intervene directly to influence interaction outcomes. In spotted hyenas, individuals with greater *recruitable* social support usually wins focal agonistic interactions (Vullioud *et al.*, 2019). Because social support has predominantly been studied in highly kin-structured species or those with nepotistic dominance hierarchies, most reported social support is 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 towards 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.

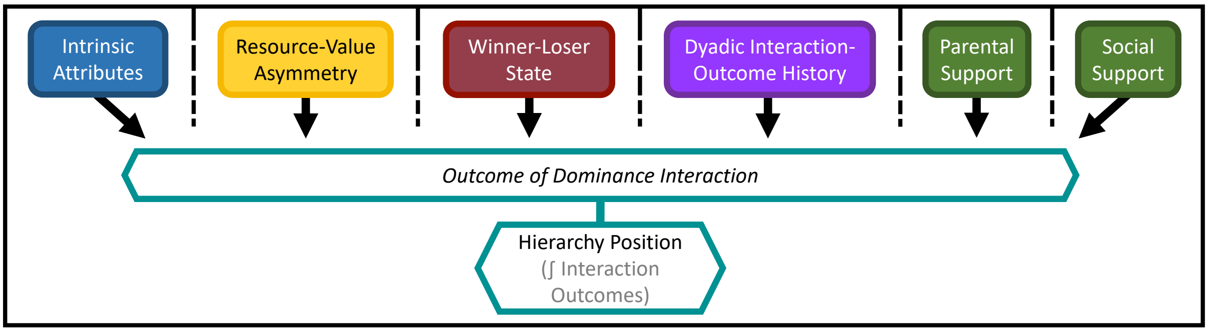

Figure 1. Six factors (filled boxes), as described in subsections II.1-5, can contribute to determining the outcomes of agonistic interactions and structure dominance hierarchies in animal groups. Factors are illustrated as partially separate to highlight that most studies to date have considered these independently when attempting to identify factors that determine the outcomes of dominance interactions (open hexagons). The colours of filled boxes 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 the primary factor determining 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 less likely to occur. Given that such differences in the presence/absence of factors across species are unlikely to change on the timescale relevant to dominance hierarchies (i.e. a few generations), 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 depends on the dyadic *difference* in that factor between two contesting individuals (Beacham, 1988). For example, the body size (an intrinsic attribute) of domestic pigs is more influential in determining interaction outcomes when a greater variation in body size exists (McBride, James, & Hodgens, 1964; Meese & Ewbank, 1973). Another clear illustration is provided 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-level factors with greater inter-individual variation within groups will have greater relevance to individuals' positions in dominance hierarchies (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). However, existing conceptual frameworks of social dominance do not explicitly consider such feedback loops with the exception of winner-loser effects which are inherently a feedback process (but see Hobson & DeDeo, 2015). Many studies on the factors underpinning dominance are correlational—often a snapshot of a dominance hierarchy and inter-individual variation in some trait—and so may not capture causal mechanisms. Experimental studies are often of short duration, which does not allow the tracking of individuals' states and dominance relationships over time. The notion of feedback, especially positive in nature and to factors such as growth or size, was raised in early studies of dominance (Magnuson, 1962; Würdinger, 1975; Black & Owen, 1987). These ideas, however, were generally not taken up more widely by other researchers.

Few studies integrate multiple, interconnected factors that affect interaction outcomes. This is likely due to the logistical challenges associated with studying multiple factors at once, and the fact that different factors could operate at different life-stages, thereby introducing temporal dependencies. Moreover, the factors determining dominance interaction outcomes have sometimes been implied to be mutually exclusive explanations of winning or losing in animal contests (e.g. winner-loser effects versus 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 feedback from interaction outcomes. In this section, we outline some of the potential feedback loops that link interaction outcomes back to the factors that determine them and, thereby, different factors to one another. While studies of complete feedback loops are largely absent for many factors, separate studies that demonstrate the two different halves of a feedback loop—e.g. separately demonstrating that intrinsic attributes affect dominance, and dominance affects intrinsic attributes—together make a compelling argument that feedbacks do indeed exist.

(1) Feedback to intrinsic attributes

Winning dominance interactions, or gaining high social status, may affect an individual's intrinsic attributes such as size, muscle mass or condition. This is not a novel idea, with studies published up to 60 years ago already demonstrating that differential growth exists among dominant and subordinate group members in fish (Magnuson, 1962) and geese (Würdinger, 1975; Black & Owen, 1987). Nevertheless, few studies have explicitly considered the feedback from interaction outcomes to the factors that determine them. Below, we describe some of the many routes by which interaction outcomes may generate a feedback onto intrinsic attributes.

Individuals' spatial positioning within the group during feeding activities is often influenced by their hierarchy position, such that higher-ranking individuals are positioned more optimally (Janson, 1990; Hall & Fedigan, 1997; Hirsch, 2011; Teichroeb, White, & Chapman, 2015; Heesen *et al.*, 2015; Papageorgiou & Farine, 2020). As a result, more dominant individuals may have superior feeding opportunities (Hall & Fedigan, 1997), leading to these individuals having higher rates of food intake (Rutberg, 1986; Black *et al.*, 1992; Wright, Robbins, & Robbins, 2014), better quality diets (Pusey & Schroepfer-Walker, 2013), or reduced energy expenditure (Wright *et al.*, 2014). However, the magnitude of such asymmetries in resource access may depend on the distribution of food resources (Whitten, 1983; Harcourt, 1987; Saito, 1996; White *et al.*, 2007). When asymmetries in food access between dominant and subordinate individuals exist, feedback from dominance—which we consider to be the result of many, integrated interaction outcomes—to intrinsic attributes can be expected to emerge. Simply put, higher-ranking individuals that have greater food or net energy intake rates are expected to have faster growth (and thus larger size) or superior body condition.

Empirical examples of feedback from dominance-related food access to differential growth primarily come from studies of 'growth depensation' in fish, in which initial dominance relationships are often largely determined by intrinsic attributes such as size (Abbott, Dunbrack, & Orr, 1985). For example, in rainbow trout, dominant individuals occupy the most optimal feeding positions, resulting in greater growth rates relative to subordinates (Metcalfe, 1986). Another example is provided by the redbelly tilapia *Tilapia zillii*, where dominant individuals are the first to feed and subsequently grow faster (Koebele, 1985). Similarly, when food is limited, Japanese rice fish *Oryzias latipes* chase smaller (subordinate) individuals away from food, thereby gaining disproportional access to food and experiencing faster growth rates (Magnuson, 1962). Thus, dominance-related access to optimal feeding positions, or simply the consumption of contested food by winners, can generate feedback to intrinsic attributes via differential growth rates among winners and losers.

Feedback from interaction outcomes to intrinsic attributes could also occur via mechanisms completely unrelated to food access. 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 (central) 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), likely allowing greater energy preservation, via thermoregulatory benefits, which can then be invested into maintaining dominance. Optimal roosting positions can thus provide a further feedback mechanism from interaction outcomes to intrinsic attributes.

A more extreme example of a feedback mechanism is 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 subordinate individuals regulate growth rates to maintain size differences with dominant individuals to avoid conflict (Buston, 2003; Wong *et al.*, 2008). Strategic growth thus allows dominants to regulate factors determining future interaction outcomes while enabling subordinates to avoid conflict, resulting in existing dominance relationships to be maintained.

Feedback from interaction outcomes can also occur to badges of status, a form of intrinsic attribute that signals quality or size through the size or colouration of a particular body part (Thompson & Moore, 1991; Tibbetts & Dale, 2004; Chaine *et al.*, 2018). Dey, *et al.* (2014) experimentally altered the perceived size of frontal shield ornaments (i.e. status badge) of pukeko *Porphyrio porphyrio* *melanotus,* which affected the aggression individuals receive. As a result, individuals' actual frontal shield size decreases in manipulated, but not unmanipulated, individuals (Dey *et al.*, 2014), presumably due to the change in received aggression. The outcomes of dominance interactions, such as receiving aggression, may thus affect to intrinsic attributes, which in turn affect individuals' future interaction outcomes via processes including strategic growth, changes to status badge expression or asymmetrical access to resources such as food or roosting sites.

(2) Feedback to resource value

The outcome of a previous interaction can, by modulating access to a resource, influence the value of a similar resource in a subsequent interaction, and thereby alter contest investment and resulting interaction outcomes (Enquist & Leimar, 1987; Arnott & Elwood, 2008). One scenario in which this can occur is in contests over food items. As losers are likely to be more hungry, having not gained access to a contested food item, they value food in a subsequent contest more highly, and increase their future contest investment accordingly (Arnott & Elwood, 2008). Therefore, the outcome of a previous interaction (losing) feeds back (via perceived resource value and related contest investment) to the outcome of a subsequent interaction (enhanced winning probability). Explicit examples of this feedback mechanism are scarce, with only part of the pathway—from hunger state to interaction outcome, but not from losing an interaction to being hungry—are typically demonstrated (e.g. Nosil, 2002). It is important to note that there may be substantial practical difficulties associated with quantifying dynamics of resource-value asymmetries in natural animal groups, especially as resource value to a focal individual likely fluctuates continuously with the individual's state and context. This loop, from interaction outcomes to resource-value asymmetry via differential access to contested food, represents a form of negative feedback—in contrast to the majority of feedback pathways we discuss here, which are predominantly positive.

Feedback from interaction outcomes to resource value can also occur in other contexts. Owner-intruder dynamics represents one such case. Here, the winner of an initial contest becomes the owner in a subsequent fight. Feedback exists because individuals value a resource they ‘own’, such as a burrow or territory, more highly than an intruder does, meaning that owners should invest more highly in contests for the resource (Maynard Smith & Parker, 1976; Enquist & Leimar, 1987). Accordingly, residents, or owners, typically win the majority of contests when faced with an intruder (Nosil, 2002; Fuxjager *et al.*, 2009; Umbers, Osborne, & Keogh, 2012; Yasuda *et al.*, 2020), and this winning propensity often increases with ownership time (Krebs, 1982; O’Connor *et al.*, 2015). Thus, effects of prior interactions on resource value can represent both positive and negative feedback loops.

(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 that, in turn, influences the probability of that individual winning the latter interaction. As feedback is implicit in winner-loser effects, studies finding winner-loser effects provide ample evidence of this feedback pathway (e.g. Beaugrand, *et al.*, 1996; Schuett, 1997; Martin *et al.*, 1997; Chase *et al.*, 2002; Huhman *et al.*, 2003; Dugatkin & Druen, 2004; Kasumovic *et al.*, 2010; Garcia *et al.*, 2014; Franz *et al.*, 2015; Trannoy *et al.*, 2016; Laskowski *et al.*, 2016).

Winner-loser effects can cause 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). In reality, however, multiple feedback loops are likely to be acting simultaneously. Therefore, the feedback implicit in winner-loser effects has the potential to amplify the results of initial interaction outcomes that could have been determined by other factors (e.g. an intrinsic attribute or third-party support). For example, winner-loser effects can be generated by staging fights among individuals with large size differences—such that the larger individual wins and smaller loses—after which individuals may be involved in size-matched contests in which previous winners win and previous losers lose (Hsu *et al.*, 2006; Laskowski *et al.*, 2016). Initial interaction outcomes that are unrelated to winner-loser effects may thus—via the feedback of winner-loser effects—determine individuals' dominance trajectories.

(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 a specific dyad* are of importance. Evidence here comes from studies that demonstrate that dyadic interaction-outcome history affects future outcomes, such as via lower levels of aggression among individuals that have recently or previously interacted. Two different methodological approaches provide evidence for such feedback. The first approach comprises studies that generate—and then test the importance of—dyadic interaction-outcome history via a two-part experimental design, which therefore provide direct evidence for this feedback. For example, in rainbow trout, aggression is lower among a pair of individuals that previously interacted, relative to pairs of unfamiliar individuals (Johnsson, 1997). Similarly, in American lobsters *Homarus americanus*, losers of an initial fight avoid fighting when repaired with the same opponent, yet actively engage in aggressive encounters when paired with an unfamiliar previous winner (Karavanich & Atema, 1998). Furthermore, in hermit crabs, losers of an initial interaction show a lower tendency to initiate contests—and when they do initiate they give up sooner—when repaired with the previous opponent vs an unfamiliar individual (Yasuda *et al.*, 2014). In the second methodological approach, studies relate contest behaviour and outcomes to 'familiarity', where individuals in familiar pairs come from the same group and those in unfamiliar pairs from different groups. As an example, in juvenile Atlantic salmon *Salmo salar*, losers display submissive body darkening after minimal contest escalation when paired with an individual they were previously housed with (in groups of 8) but not when paired with an unfamiliar conspecifics (O'Connor, Metcalfe, & Taylor, 2000). In golden-crowned sparrows, manipulating a status signal reverses the dominance relationship among unfamiliar but not familiar pairs of individuals (Chaine *et al.*, 2018).

The degree of prior social interaction was, however, not quantified or experimentally generated as in the first set of studies, above. Instead, prior social interactions are assumed between individuals caught at the same location and time as these are likely flockmates and so familiar (Shizuka *et al.*, 2014). Thus, contest behaviour in studies of the second type provide less firm support for dyadic interaction-outcome history as familiarity and prior interactions are not synonymous, and results could alternatively be driven by group-level characteristics or kinship markers (Tibbetts & Dale, 2007).

An interesting question is how past interactions are weighted. For example, in contesting green anoles, losers reduce aggression when re-paired with the same opponent (relative to an unfamiliar opponent) three days after the initial contest, but not after ten days (Forster *et al.*, 2005). Similarly, the rate of aggression among two three-spined sticklebacks increases with time spent apart, ranging from zero to four weeks (Utne-Palm & Hart, 2000). Furthermore, in rainbow trout, after an initial interaction, aggression between pairs of individuals that had previously interacted increased with time spent separated—but not between unfamiliar individuals (Johnsson, 1997). Thus, more recent interaction outcomes often have a stronger effect on future interaction outcomes within the dyad, as it is likely that the reliability of information regarding relative competitive abilities decays with time.

The feedback to dyadic interaction-outcome history can have consequences for other factors and feedback loops. For example, as with winner-loser effects, this feedback loop likely reinforces the effects of other factors on interaction outcomes and therefore represents a form of positive feedback that stabilises dominance relationships. Thus, this feedback loop should amplify dyadic differences in other factors, which further increases the probability that winners carry on winning and losers carry on losing. Additionally, this feedback loop should 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 dyadic interaction-outcome history increases in importance over time.

(5) Feedback to social support

An individual's position in the dominance hierarchy, determined by previous interaction outcomes, often modulates the degree of social support it receives. This could also be thought of as 'downward causation', where a higher-level feature (i.e. position in the dominance hierarchy) influences the behaviour of lower-level components (i.e. support received, Flack, 2017). Examples of such rank-dependent social support come primarily from mammals. In spotted hyenas, individuals intervening in ongoing agonistic interactions typically support the individual higher in the hierarchy (Smith *et al.*, 2010). Similarly, third-party individuals in vervet monkeys *Chlorocebus pygerythrus* consistently support the more dominant individual when joining (dyadic) agonistic interactions (Borgeaud & Bshary, 2015). Likewise, when intervening in ongoing dyadic disputes, female savannah baboons *Papio cynocephalus* predominantly provide support to the individual positioned higher in the hierarchy (Silk, Alberts, & Altmann, 2004). While current evidence comes primarily from hyenas and primates, ravens have also been shown to preferentially support higher-ranking group members (Fraser & Bugnyar, 2012). Taken together, these studies suggest that the preferential provisioning of support to higher-ranking group members (i.e. winners) can act as a positive feedback loop, ultimately stabilising dominance relationships and hierarchies (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 solely 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.

Importantly, the feedback loops described above could act in opposite 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 by the winner, which therefore represents negative feedback to resource-value asymmetry; however, the feedback to winner-loser state will be positive for the winner, as winning the initial interaction will place the individual in a winner state. While the majority of feedback loops are likely positive (see Table 1), how different feedback loops operate together, and over what temporal scales, remains unknown and warrants theoretical and empirical study.

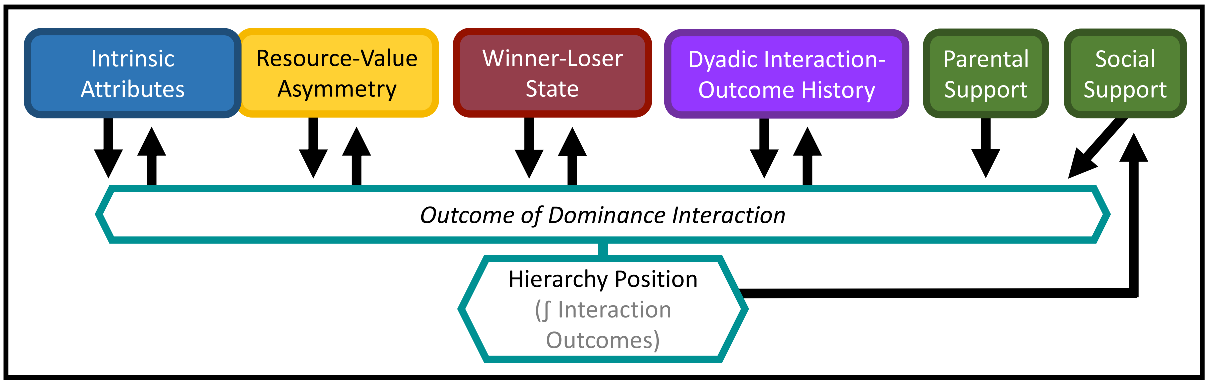

Figure 2. Outcomes of dominance interactions can feed back to the factors that determine outcomes of future dominance interactions. By combining sections II and III, we can create a conceptual dominance framework that reveals numerous potential feedback loops between interaction outcomes and the factors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

Table 1. Expected nature of each feedback loop or feed-forward mechanism discussed in sections III and IV. Feedback loops and feed-forward processes described here each relate to an arrow in Fig. 3 and represent a testable hypothesis with varying levels of empirical support. Note that not all processes illustrated here will be equally important to all taxa.

Type	From	To	Expectation	Description
Feedback loop	Hierarchy position	Social support	+	Individuals higher in the hierarchy receive better/more frequent support
Feedback loop	Interaction outcome	Intrinsic attributes	+	Winners of previous food-resource contests assimilate more food and thus enhance energy levels/body condition

				etc. for subsequent interactions
Feedback loop	Interaction outcome	Resource-value asymmetry	+ / -	Feeding opportunities: winners are more satiated, and so invest less heavily in future interactions, *vice versa* for losers Ownership: owners, having already invested in the resource, invest more heavily in subsequent interaction
Feedback loop	Interaction outcome	Winner-Loser state	+	Winners of a previous interaction will be in a 'winner state' in a subsequent interaction, enhancing their probability of winning, and *vice versa* for losers
Feedback loop	Interaction outcome	Dyadic interaction-outcome history	+	Winners establish that they can win against the specific opponent (and vice versa for losers), and so subsequent interactions are easily settled as losers should avoid wasting resources in interactions they are unlikely to win
Feed-forward mechanism	Parental intrinsic attributes	Offspring intrinsic attributes	+	Larger/more aggressive parents produce larger/more aggressive offspring. Similarly, larger parents or those in better condition reproduce earlier, producing offspring that are older and more developed relative to the rest of the cohort
Feed-forward mechanism	Parental hierarchy position	Offspring intrinsic attributes	+	Offspring of high-ranking parents gain superior access to resources and thus enjoy a higher-quality development
Feed-forward mechanism	Parental hierarchy position	Parental support	+	Offspring of high-ranking parents gain better/more frequent support relative to offspring of low-ranking parents
Feed-forward mechanism	Parental social support	Offspring social support	+	Social inheritance of social relations and associated support.

IV. Parental effects on the factors determining 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 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 East *et al.*, 2009; 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).

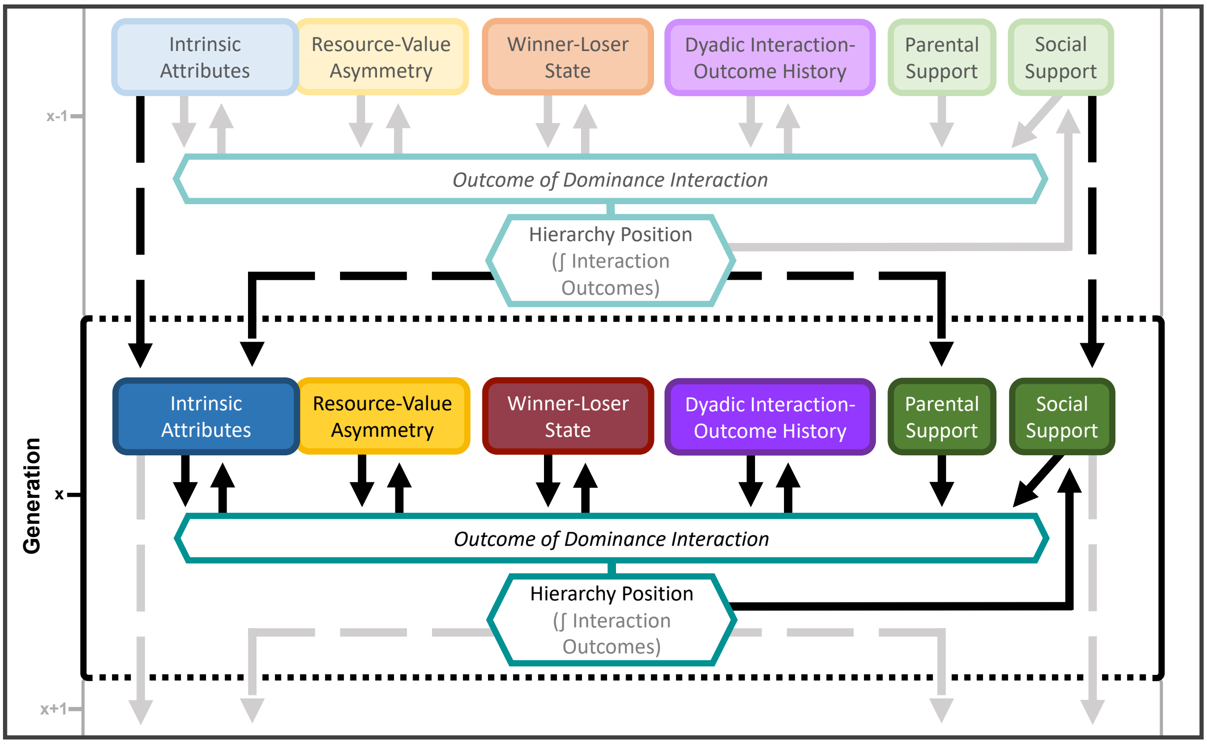

Figure 3. Integrating transgenerational (feed-forward) mechanisms with factors determining interaction outcomes and their feedbacks. Interaction outcomes and the factors that determine them (Fig. 2) that operate in a previous generation (x-1) can affect interaction outcomes in a focal generation (x). Potentially important 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. Interaction outcomes and the factors determining them in the focal generation are coloured as in Fig. 1 & 2, while those of the parental generation are lighter.

(1) Parental effects on offspring intrinsic attributes

Parents can influence the intrinsic attributes of offspring 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, 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 that 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). Similarly, 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). In barnacle geese *Branta leucopsis*, more aggressive parents provide superior parental care (e.g. flee the nest less and rear more offspring), meaning that goslings of aggressive parents tend to be larger and dominant over goslings raised by less aggressive parents (Black & Owen, 1987). In meerkats, the offspring of dominant females 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. Accordingly, because access to food resources—especially in early life—has long-term consequences for an individual's intrinsic attributes (Richner, 1992), there is widespread empirical evidence for parental effects having potential 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 the hormone levels that developing young are exposed to (Mousseau & Fox, 1998). Exposure to higher androgen levels is associated with 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). Similarly, the above findings that offspring of dominant meerkats grow quicker could arise from differences in the timing of reproduction, a prenatal parental effect, for example if the offspring of dominant individuals emerge earlier and are larger than their cohort mates (English *et al.*, 2014). 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, programming of offspring development, and the timing of reproduction.

(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 (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, 2021), 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 may 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) outline how researchers can 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 that a similar approach is applicable for understanding the feedback loop between interaction outcomes and a particular factor.

Methodological developments in the field of dominance have provided increasingly advanced analytical tools crucial for studying hierarchy dynamics. Elo scores were introduced to behavioural ecology two decades ago and provide a solid platform for such developments. Here, at any particular point, an individual's score relative to that of conspecifics reflects 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 useful for capturing temporal properties of dominance hierarchies. 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 interacting individuals, 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.

Concepts from complex systems sciences are already being integrated in studies of dominance. For example, scales of organization, compression, and emergence have been suggested to allow researchers studying dominance to better conceptualise social complexity (Fischer *et al.*, 2017; Hobson *et al.*, 2019). Moreover, the use of complex systems approaches to study the effect of third-party intervention (Flack, de Waal, & Krakauer, 2005b) on levels of aggression and socio-positive interactions (Flack, Krakauer, & de Waal, 2005a) as well as social niches (Flack *et al.*, 2006) was pioneered in the 2000s using pigtailed macaques *Macaca nemestrina*. More widespread implementation of approaches from complex systems sciences in studies of social dominance may prove to be a fruitful tool for understanding the mechanisms that underpin hierarchy structure and stability.

(2) Integrating different interaction types

There is emerging evidence that within a particular species different types of dominance interactions (such as chases, displacements or submissive interactions) may be expressed differently and not interchangeably (van der Marel *et al.*, 2021; Dehnen *et al.*, 2021). Existing approaches allow researchers to vary the contributions—i.e. to changes in Elo scores—of different types of interactions (e.g. according to intensity, Newton-Fisher, 2017). However, multi-layer networks provide a framework that allows different types of interactions to be modelled explicitly (Finn *et al.*, 2019). In multi-layer networks, each layer contains interactions (edges) among individuals (nodes) for a particular type of dominance interaction, such that there may be, for example, a ‘submissive’ interaction layer and a ‘displacement’ interaction layer. Given that nodes connect layers (i.e. each individual is present in every layer), this 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, intrinsic attributes) predict the patterns of interactions they express or receive. In addition, 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 extended 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). One approach has been to use cases of natural adoptions which allow for correlational analyses (East *et al.*, 2009). Nevertheless, disentangling causal pathways of parental effects remains a methodological challenge in natural systems and will require experimental manipulations.

One solution may be to broaden research to species in which parental effects can be manipulated to experimentally tease apart potential mechanisms. Birds represent one taxon that may 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). Moreover, the breeding biology of birds allows the manipulation of the timing of breeding (Verhulst & Nilsson, 2008) to alter the relative age and developmental stage of cohort mates. Lastly, clutch or egg removal can enable researchers to alter parental investment (Nager, Monaghan, & Houston, 2000). 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, the tools to investigate causal mechanisms underpinning transgenerational feed-forward effects already exist.

Manipulating the factors discussed in section II will also be facilitated by the development and availability of novel technologies. ‘Smart feeders’, for example, can selectively open depending on the tagged individual(s) present (Ibarra *et al.*, 2015; Firth, Sheldon, & Farine, 2016; Bridge *et al.*, 2019) and might be used to not only allow (or prevent) particular individuals to feed, but also vary the nutritional content of food items individuals have access to. Thereby, 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). Other 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). Ultimately, experimental studies will play a major role in unpacking the complex feedback and feed-forward dynamics that underpin dominance outcomes.

VI. Key directions

(1) Feedback and variation in factors that determine interaction outcomes

If positive feedback exists between dominance and its determinants, we would predict that variation in these determinants increases. For example, winner-loser effects are by definition absent in individuals prior to their first agonistic interaction, yet emerge and strengthen over time (Dugatkin, 1997; Trannoy *et al.*, 2016; Laskowski *et al.*, 2016; Hobson, Mønster, & DeDeo, 2021). Similarly, in groups of domestic pigs *Sus scrofa domesticus* hierarchy position does not relate to body mass when groups are newly formed (Meese & Ewbank, 1973), yet in well-established groups hierarchy position is correlated with mass (McBride *et al.*, 1964). Thus, positive feedback, over time, can give rise to differences in the factors that determine interaction outcomes.

One way in which empiricists might demonstrate the existence of feedback is by comparing how variation emerges in social groups where feedback mechanisms are experimentally enabled or disabled, or where the strength of the feedback is manipulated. Feedback to intrinsic attributes may, for example, emerge via monopolisable food resources (Magnuson, 1962; Koebele, 1985; Metcalfe, 1986). By experimentally controlling how monopolisable food is—e.g. via dispersed vs clumped food resources (Whitten, 1983; Harcourt, 1987; Saito, 1996; White *et al.*, 2007)—researchers could vary the strength of feedback, i.e. from inter-individual differences in feeding rates to differences in size, which in turn affect the outcome of dominance interactions. Thereby, researchers might find that greater variation in size, and associated increases in the strength of winner-loser effects or changes in dyadic interaction history, arises in groups with stronger feedback to intrinsic attributes. Laboratory systems, especially those in which food monopolisation is easily manipulated and in which size—an intrinsic attribute—influences dominance, such as in many fish species, may provide especially fertile grounds for such studies. Additionally, experimental manipulation of a factor important to determining interaction outcomes, combined with tracking the effects on hierarchy dynamics over time, will allow researchers to separate positive from negative feedback loops.

Some form of 'brake' that limits runaway positive feedback may also act in many species, as they do in other dimensions of biological systems such as population density regulation, given that we don't find ever growing asymmetries in at least some factors (e.g. size) among group members. Such brakes may be unrelated to dominance. For example, morphological limits, which individuals cannot exceed despite a rich adult diet, may be set in early life (Poças, Crosbie, & Mirth, 2020). However, braking mechanisms could also be directly related to dominance. For example, when dominant vulturine guineafowl *Acryllium vulturinum* monopolise food patches, subordinates are excluded and accumulate at the periphery of the patch. Once a critical number of subordinates are excluded, the subordinates leave and forage elsewhere and dominant individuals then follow (Papageorgiou & Farine, 2020). Therefore, the degree to which dominant individuals can monopolise food resources may, once reaching a certain threshold, limit the effect this has on asymmetries in food access and thus also the strength of feedback. The quantification of changes in the strength of feedback loops over time, e.g. whether negative feedback loops or brake mechanisms kick in and reduce variation in factors important to dominance—previously generated by positive feedback—will therefore require long-term studies.

(2) The importance of social structure to feedback loops

The characteristics of animal groups vary considerably both within and between species (Prox & Farine, 2020). For a particular species, the social tendency, i.e. the degree to which individuals spend time together, and the level of entry restriction, i.e. how open or closed groups are to individuals joining (see Ward & Webster, 2016), are two axes of social structure that might be important in determining the strength of the feedback loops described above. A group's social tendency influences the frequency of interactions and instances of competition for resources, by which feedback occurs. Thus, feedback loops in groups or species with lower social tendency—where group members are more diffuse—may be weaker. Given that the majority of feedback loops we describe here are likely to be positive, comparative studies of species or social groups might find that the stability of the dominance relationships (i.e. either at the group or dyadic level) varies with social tendency. Specifically, groups or species with a higher social tendency might have more temporally-stable hierarchies with individuals occupying more defined ranks.

The level of entry restriction may also be important in determining the degree to which feedback loops influence individuals in a social group: feedback effects are likely to be stronger in closed groups because individuals are exposed to the feedback process over a longer duration without interruptions from new group members. Hence, if positive feedback loops cause asymmetries in winning propensities to widen among dominant and subordinate group members over time, then dominance relationships and hierarchies are likely to be more stable in closed groups. In addition to investigating the roles of group social tendency and the level of entry restriction on dominance stability empirically, agent-based models of dominance (e.g. Hemelrijk, 2000), in which groups are made to vary in social cohesiveness, may shed further light on how social structure affects hierarchy stability via feedback processes.

(3) Interconnected feedback loops and timescales

Orderly, or linear, hierarchies are those in which there are more transitive triads of individuals than expected by chance; in a perfectly orderly hierarchy, each individual dominates all individuals below itself (Shizuka & McDonald, 2012). Such orderly hierarchies are found across diverse taxa (McDonald & Shizuka, 2012), which is probably due to most feedback loops being positive in nature (Table 1) and thereby widening asymmetries in the factors determining interaction outcomes (and therefore dominance) with repeated interactions. One question is whether different pathways vary in their contributions to hierarchy orderliness over time. This is expected because the rate at which feedback takes place should vary between different feedback mechanisms. For example, winner-loser effects (and dyadic interaction-outcome history more locally) can set up rapid positive feedbacks, with the emergent hierarchy order being strengthened from one interaction to the next. Nevertheless, if group membership is large or fluid (so that winners could often encounter winners, placing one of these in the loser state), then winner-loser effects or dyadic interaction-outcome history may not act so intensely. By contrast, the feedback between interaction outcomes and intrinsic attributes should act more slowly, as differences in intrinsic attributes generally emerge over longer timescales. For example, winner-loser effects emerge immediately (Chase, Bartolomeo, & Dugatkin, 1994) while assimilating a piece of contested food into muscle mass takes much longer. Once emerged, however, differences in intrinsic attributes—generated by feedback—likely last for longer, thereby driving more persistent hierarchy orderliness. For example, winner-loser effects and dyadic interaction-outcome history might be initially important but, over time, interaction outcomes also drive differences in intrinsic attributes. Thus, while multiple feedback loops could drive hierarchy structure, the contributing feedbacks may not always be apparent and change over time.

Factors might also vary in their contributions according to the time since the last interaction. While emerging immediately, winner-loser effects and dyadic interaction outcome history are not long-lived without further reinforcement (see sections III.3-4). In contrast, differences in intrinsic attributes are likely to persist for longer over periods devoid of reinforcement through further interactions. Thus, the relative importance of different feedback mechanisms to hierarchy orderliness likely varies with the individual-level interval between interactions in animal groups. Accordingly, monitoring outcomes of interactions in which a) the expected contribution of dyadic interaction-outcome history (or winner-loser effects) and intrinsic attributes act in opposing directions, and b) which differ in time since the last interaction, could reveal the relative importance of different feedbacks to hierarchy orderliness as a function of time.

(4) The importance of stochastic phenomena for individuals' hierarchy positions

(a) To what extent do stochastic outcomes early in the interaction history influence individuals' dominance trajectories?

In any interaction, there exists some stochasticity that could cause the outcome to oppose the expected directionality arising from asymmetries in the factors described in section II (i.e. the expected winner loses). As positive feedback loops act to stabilise interaction outcomes over time, we expect that—when more (influential) feedback loops are positive—stochastic interaction outcomes early in a group's history, or after an individuals' introduction, will be amplified by subsequent interactions and affect individuals' dominance trajectories. Because positive feedback loops widen asymmetries in winning abilities among group members, the frequency of interactions in which the outcome is unexpected due to stochastic effects is likely to be much lower in well-established groups. Accordingly, the more positive feedback in a system, the stronger the effect of unexpected interaction outcomes due to stochasticity that occur early in a group's history. Stochastic effects may therefore be most important when individuals join groups (i.e. in early life or after immigration) or when groups form. Given the challenges of studying processes such as immigration and group formation, theoretical studies might be required to guide future empirical work. Specifically, such studies could explore how social tendency and the strength of feedbacks makes dominance hierarchies robust or susceptible to being influenced by stochastic interaction outcomes.

(b) How stochastic events and resultant demographic changes impact individuals' dominance trajectories

Stochastic events might also provide natural experiments that allow for the study of feedbacks as changes in group membership passively influence individuals' hierarchy positions and thereby alter feedback loops. Examples of such processes include interspecific killing (Palomares & Caro, 1999), natural disasters (Testard *et al.*, 2021) or predation events. For example, in a troop of olive baboons *Papio anubis*, a bovine tuberculosis outbreak caused primarily aggressive males to die which dramatically altered the group composition, leaving only adult females and less aggressive males (Sapolsky & Share, 2004). Similarly, spotted hyenas may be targeted by pastoralists using poisoned carcasses (Holekamp *et al.*, 1993), causing fatalities of high-ranking individuals as these gain priority access to food (Watts & Holekamp, 2009). One consequence of such changes in group composition is that individuals experience passive changes in hierarchy positions (Strauss & Holekamp, 2019b), which can be expected to alter the outcomes of future dominance interactions. For example, mid-ranking individuals might move to the top of the hierarchy, which then confers the benefits of dominance on these individuals. Thus, by altering the interactions that individuals experience, demographic changes could disrupt feedback loops, providing an opportunity to gain some more insights into how they operate.

(5) The potential for feed-forward mechanisms

Does the contribution of feed-forward mechanisms in structuring dominance hierarchies vary with social structure? Parental effects on offspring intrinsic attributes are ubiquitous (Bernardo, 1996; Mousseau & Fox, 1998), yet few studies have linked parental effects to offspring hierarchy position in early, and especially later, life. To date, evidence comes primarily from societies with high entry restriction (i.e. closed societies), such as in primates (Maestripieri, 2018) and hyenas (Holekamp & Smale, 1993; Smale, Laurence, & Holekamp, 1993; Engh *et al.*, 2000; East *et al.*, 2009). This could be because such social structures are more conducive to parental effects on offspring dominance, as parents can readily assess the level of competition that their offspring might face. Alternatively, this bias could be because it is easier to study such effects in closed societies where individuals can be readily followed over significant portions of their lives. However, to what degree parental effects influence offspring dominance in low-entry restriction societies is largely unclear (but see Black & Owen, 1987; Eising, Müller, & Groothuis, 2006; Weiß *et al.*, 2011). In such societies, parents likely have much less information on the social environment that offspring will experience, and individuals' dominance trajectories may also be more susceptible to stochasticity (see section VI.6a). Thus, the role of feed-forward mechanisms in determining offspring hierarchy positions in societies with low entry restriction remains to be well understood.

Understanding the importance of feed-forward mechanisms in these societies will be facilitated by the study of species in which pre- and post-natal parental effects can be manipulated. Bird societies, which vary considerably in the level of entry restriction (Papageorgiou *et al.*, 2019; Aplin *et al.*, 2021) and may be structured by dominance hierarchies (Black & Owen, 1987; Papageorgiou & Farine, 2020; Portugal *et al.*, 2020), are amenable to manipulating parental effects at various stages of reproduction (see section V.3). Likewise, insects vary considerably in social structure (Wilson, 1971; Costa, 2006), exhibit dominance hierarchies (Shizuka & McDonald, 2015) and allow for the manipulation of parental effects—which can be pre- (Lewis & South, 2012) or post-natal (Wong, Meunier, & Kölliker, 2013). Such taxa will thus aid in advancing our understanding of feed-forward mechanisms in low entry-restriction societies.

(6) Feedback from offspring to parents

While feed-forward mechanisms allow parents to impact offspring hierarchy positions, there is also the potential for feedbacks to take place wherein the offspring themselves affect the position of their parents in the hierarchy. Such feedback from offspring to parents likely occurs when individuals and their parents to co-exist in the same social group for extended periods of time, such as in plural or colonial breeders. Individuals in such species could influence the factors that determine the interaction outcomes of their parents, e.g. by lending social support. For example, spotted hyenas cubs—which always outrank their fathers—are less aggressive towards their sires than to control males (Van Horn, Wahaj, & Holekamp, 2004). Thus, in addition to transgenerational feed-forward mechanisms, transgenerational feedback, from offspring to their parents, may also exist. Given that such offspring-to-parent feedback likely occurs via social support or reduced aggression, species in which at least one sex is philopatric might be suitable systems for studying such effects.

VII. 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 aware of these feedback loops when ascribing causality to factor-dominance associations, 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 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 that allow parents to influence social dominance in offspring.

(4) We suggest that the manipulation of a factor important to interaction outcomes can, 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 echo calls to integrate approaches from complex systems sciences to the study of dominance (Flack *et al.*, 2005b, 2005a, 2006; Fischer *et al.*, 2017; Hobson *et al.*, 2019), specifically to study the effects of the various feedback loops on hierarchy dynamics.

(5) We highlight several key directions for future work and suggest approaches that might allow the testing of predictions. Experimental approaches that vary the strength of feedback will allow researchers to elucidate its role in generating variation within the group. Furthermore, social structure may determine the degree to which a group is exposed to feedback processes, and may be investigated via group- or species-level comparative studies. Moreover, stochastic interaction outcomes early in the interaction history combined with positive feedback, as well as stochastic demographic changes, can have long-term consequences for individuals' dominance trajectories and could be studied via a variety of approaches. Additionally, we urge researchers to conduct studies of transgenerational feed-forward effects in species that allow manipulations of parental effects to uncover causal mechanisms. Conducting such experiments in understudied species and across diverse social systems will also broaden our understanding of the routes by which parents can influence offspring dominance relationships and whether such effects vary with social

structure. Lastly, feedback processes may also exist across generations, given that offspring could affect factors important to parents' interaction outcomes in species with overlapping generations. 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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