SOCIAL INEQUALITY AND ITS DYNAMICS IN SPOTTED HYENAS

By

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ABSTRACT

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Organisms living in social groups incur both benefits and costs of group-living, and social inequality arises as individuals differentially experience these costs and benefits. In animals, social inequality often manifests as a dominance hierarchy, where some individuals are consistently able to dominate others during fights among groupmates. In these hierarchies, an animal's rank denotes its position in the social hierarchy, and rank mediates access to resources and reproductive opportunities in many species. In my dissertation, I examine the forces underlying the dynamics of dominance in the societies of spotted hyenas (Crocuta crocuta). I first review the current understanding of the phenomena of aggression and dominance at multiple levels of analysis. Next, I develop a framework and tools to study the dynamics of dominance hierarchies using longitudinal aggression data. I then apply this framework and methods to long-term data on spotted hyena social hierarchies to reveal the forces producing, and preventing, rank changes in these hierarchies. My results reveal how coalitionary alliances mediate change in the social hierarchy, and that intergenerational patterns in hierarchy dynamics lead to dynastic structures in these societies. Finally, I turn to the development of social rank in juveniles and examine the long-term fitness consequences of early-life variability in rank acquisition in this species. I find that transient variation in rank acquisition predicts sizeable lifetime fitness consequences for

developing juveniles, suggesting that this aspect of social development can have dramatic consequences. Overall, my research reveals how dynamical approaches to dominance can reveal the forces producing and maintaining social inequality.

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INTRODUCTION

Like other aspects of animal biology and biodiversity, social structure is a biological dimension of remarkable variety. Some animals live primarily solitary lives with minimal interaction with conspecifics, whereas others spend their entire lives surrounded by familiar groupmates. The extent to which animals live socially is typically thought of in terms of the costs and benefits associated with group living [1,2]. In most societies, however, the costs and benefits of group living are not experienced equally by all group members. Instead, social inequality arises when some individuals benefit from group living more than others do. Interestingly, the existence of such social inequality is normative among animal societies (including those of humans), but societies vary in the severity of social inequality, the mechanisms that maintain it, and the relevant dimensions (e.g., access to resources, reproduction, health) in which this inequality is most apparent.

Like most animal studies of social inequality, I employ the concept of the dominance hierarchy [3]. A dominance hierarchy is a useful abstraction that describes general patterns in the dominance relationships among pairs of individuals in a social group. These dominance relationships are characterized by consistent asymmetric outcomes of fights among group-mates, wherein one individual consistently exhibits a submissive display to the other [4,5]. In many animal societies, these dominance relationships are transitive: if A is dominant to B and B is dominant to C, A is also dominant to C [6]. When dominance relationships are transitive, a linear dominance hierarchy can be used to describe the average ability of each individual to dominate its

group-mates [7]. In this paradigm, each individual is assigned a rank, which denotes its position in the social hierarchy: individuals of high status (small rank numbers) are able to dominate many group-mates, whereas individuals of low status (large rank numbers) are dominated by most other group-mates. In the near century [3] that dominance rank has been a subject of research in behavioral ecology, it has become clear that this paradigm is a powerful tool for understanding social inequality in animals.

Most studies treat dominance rank as a static attribute of individuals, but dominance hierarchies are dynamical entities that are subject to change over time. For example, dominance hierarchies change as new individuals enter and leave the group through demographic processes. Additionally, individuals can alter previously held dominance relationships to produce changes in the structure of the dominance hierarchy, even in the absence of demographic changes. Finally, the ontogeny of dominance in juveniles is a dynamic process in which juveniles go from being socially naïve to being fully embedded in the social hierarchy by negotiating new dominance relationships with their group-mates. Although few would contest the possibility of change in dominance hierarchies, these hierarchies are most often treated as static for two reasons: 1) the short time frame over which many studies are conducted, and 2) a paucity of methodological support for dynamical treatment of these entities. Nevertheless, understanding the forces producing dynamics in dominance hierarchies can provide powerful insight into the forces influencing social inequality.

In my dissertation, I delve into the forces underlying social inequality by investigating the dynamics of dominance in the unique societies of spotted hyenas (*Crocuta crocuta*). In Chapter One, I review the current understanding of aggression,

dominance, and their intersection. This chapter follows a Tinbergian structure, in that I discuss aggression and dominance at the level of mechanism, ontogeny, function, and phylogenetic history [8].

In Chapter Two, I develop a framework and methods for studying the dynamics of dominance. First, I introduce the concept of a longitudinal dominance hierarchy, which describes a latent hierarchy as a series of rank orderings of members of a single social group over time. Next, I define and distinguish between different types of hierarchy dynamics and explain how they may be detected from a longitudinal hierarchy. I then extend established ranking methods for inferring dominance relationships to allow them to reliably infer longitudinal hierarchies. Finally, I compare the efficacy with which these extended methods identify hierarchies and their dynamics.

In Chapter Three, I apply the methodological developments of Chapter Two to understand rank changes, and their absence, in the societies of spotted hyenas. Whereas many societies appear to be structured around individual phenotypes, the societies of some animals, such as spotted hyenas, instead appear to follow arbitrary conventions determining which animals are dominant and which are subordinate. This system is highly perplexing: rank has important effects on fitness in these societies, yet the members of these societies follow these conventions reliably and apparently irrespective of individual quality. In this chapter, I find support for the hypothesis that social alliances provide structure to, and sometimes change, these "convention-based" hierarchies. I go on to demonstrate that the rare cases where individuals reverse previously held dominance relationships (i.e., "active dynamics") can have important fitness consequences. Finally, I examine the long-term effect of dynamics due to

demographic processes (i.e., "passive dynamics") to reveal intergenerational patterns in social inequality and the interaction between different types of hierarchy dynamics.

In Chapter Four, I turn to the dynamic process of rank acquisition by juveniles to understand selection on rank learning and social development. In spotted hyenas, rank is 'inherited' through a behavioral learning process that takes place during development. This process, called 'maternal rank inheritance,' is highly predictable: ~80% of juveniles acquire the exact rank predicted. Crucially, the predictable nature of rank acquisition in these societies enables the study of rank acquisition independently of the rank individuals ultimately attain. Here, I extend and apply an existing ranking method to quantify the state of rank acquisition by juveniles at a crucial phase of social development. Despite variability in rank acquisition in juveniles, most of these juveniles come to attain the exact rank expected of them according to maternal rank inheritance. Nevertheless, variation in rank acquisition predicts long term fitness consequences spanning the lives of these individuals: juveniles 'underperforming' their maternal rank at the end of their den dependent period show reduced survival and reduced lifetime reproductive success. Finally, I present evidence that this variability in rank acquisition in early life can be a source of early life adversity, and that multiple sources of early life adversity have cumulative, but not compounding, effects on fitness.

The work presented in these chapters has been prepared as part of a collaborative effort by myself and others, and has been (or will be) published with multiple credited authors. As a result, I use 'we' throughout the dissertation to describe the work conducted here.

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CHAPTER ONE

AGGRESSION AND DOMINANCE: AN INTERDISCIPLINARY OVERVIEW

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ABSTRACT

Aggression is ubiquitous among animals, and contest outcomes in many gregarious species yield societies structured by dominance hierarchies. Recent results from a variety of disciplines have laid the groundwork for an integrative view of aggression and dominance, ranging from their physiological underpinnings to their evolutionary histories. Here we use Tinbergen's four levels of behavioral analysis to summarize our current understanding of aggressive behavior and dominance relationships. First, we discuss the role of epigenetic effects in the ontogenetic emergence of aggressive and rank-related phenotypes, and summarize how these phenotypes are mediated by endocrine and nervous system activity. We briefly review recent work on the functions of aggression and dominance hierarchies in animal societies, and then consider their phylogenetic history. Finally, we review methodological encumbrances to the study of dominance, and consider the unique evolution of aggression and dominance relationships in humans.

INTRODUCTION

Aggressive behavior occurs ubiquitously in the animal kingdom, in creatures ranging from sea anemones to humans. Aggression can take many different forms, so we define it here as harmful, potentially harmful, or threatening behavior that is directed towards conspecifics, and tends to increase the distance between an attacker and its opponent. Although aggressive behaviors occur in myriad contexts, we will refer mainly to behaviors occurring in association with actual or anticipated competition for resources. In contests over limited resources, success is often determined by aggressive behavior. In many gregarious animals, repeated aggressive interactions among members of a social group result in stable asymmetric relationships between individuals; an emergent property of these repeated interactions is a dominance hierarchy that structures the entire society [1]. Higher-ranking animals consistently defeat lower-ranking animals in agonistic encounters [2], although the most dominant individuals are not necessarily the most aggressive [3,4]. Dominance-related behavior depends on recognition of social status and the intentions or motivations of potential opponents [5,6,7]. Although aggression is usually necessary for hierarchy formation, once established, a stable hierarchy can suppress further aggression and unwanted fights among group members [1]. An individual's position in a dominance hierarchy usually determines its priority of access to key resources. Social rank can thus have profound effects on health, aging and fitness measures [e.g., 8, 9, 10]. Other work has also revealed important effects of an individual's rank position on many other aspects of its biology, including its circadian rhythms [11] immune function [12, 13], brain development [14], and patterns of gene expression in the adult brain [15, 16]. Here we

frame our review of aggression and dominance in the context of Tinbergen's [17] four levels of analysis in the study of behavior. Thus we highlight recent insights regarding the ontogenetic development of aggression and dominance relationships, the physiological and genetic mechanisms mediating these phenomena, their adaptive significance, and their phylogenetic history.

Ontogenetic development of aggression and dominance

Development of aggressive behavior

Early rearing conditions have powerful effects on adult aggressive behavior in animals as diverse as humans [18], pigs [19], rodents [20] and birds [21]. Longitudinal studies initiated at birth in humans show that physical aggression is more frequent in early childhood than at any other time during the life-span, and that high levels of aggression in adults often ensue from failure to develop the ability to inhibit aggressive tendencies [18]. Infant pigs that experience higher rates of aggression from littermates while suckling mature to be more aggressive after weaning [19]. Adverse rearing conditions can put individuals on a chronic trajectory of aggressiveness that persists from early life to adulthood. Studies of rodents, humans and other primates show that various types of early adversity, including repeated maternal separation and neglect, strife between parents, post-weaning social isolation and peri-pubertal stress, can each independently induce the development of deviant forms of adult aggression, including mismatches between provocation and response, attacks on inappropriate targets, and deficits in social signaling. In rodents, primates and zebra finches, both post-natal and adolescent phases of development represent sensitive periods during which social

conditions have lasting effects on adult aggression [20, 21]. Interestingly, spontaneous aggression can even be elicited in robots "raised" under adverse environmental conditions [22].

In addition to early rearing conditions, several other factors have been found to shape adult aggression including an animal's sex, its intrauterine position, its personality traits, its maternal rank, its mother's behavior, and population density. Ontogenetic trajectories of aggressive behavior are often sexually dimorphic with respect to the age at which peak aggression occurs, which types of conspecifics are targeted, and which individuals receive the most aggression [e.g., 23, 24, 10, 25]. Intrauterine position affects both aggression and dominance among female *Octodon degus* [26]. It is becoming increasingly clear that aggressiveness and the ability to dominate conspecifics often correlate positively with other personality traits, including boldness, exploration and stress reactivity [27]. Maternal behavior and maternal rank also profoundly affect offspring aggressiveness in creatures as diverse as monkeys [28] and fish [29]. Rates of aggression are often highest in the densest populations [e.g., 23, 30].

Development of dominance and dominance hierarchies

In most gregarious birds and mammals, the ontogeny of dominance relationships generally conforms to one of two major patterns. In the most common case, dominance is determined by intrinsic factors such as body size, fighting ability, personality traits, or other attributes that directly affect the ability to win fights [31, 32]. In these cases, dominance status fluctuates over time and in association with changing competitive ability and health. Alternatively, some primates and spotted hyenas form nepotistic

societies, in which dominance status, particularly among members of the philopatric sex, is highly influenced by familial rank. In these societies, dominance acquisition begins in infancy and involves coalitionary support from kin [e.g., 33, 34].

Although social status is largely influenced by either familial rank or intrinsic attributes, theoretical and empirical evidence suggests that emergent social properties also influence the ontogeny of dominance. The 'social dynamics' hypothesis posits that dominance ranks emerge from self-organization dynamics such as winner-loser effects or highly localized social network properties, even in the absence of individual differences in specific attributes [35, 36, 37]. Winner-loser effects are well-documented forms of learning in which victorious individuals subsequently behave more aggressively, whereas losers behave more submissively [38, 39, 40]. Historically, most work on these effects has been conducted in lab settings with experimental designs that artificially eliminate or minimize individual differences [e.g., 41]. However, methodological advances have permitted testing of the social dynamics hypothesis in unmanipulated animal groups [42, 43]. Results suggest that localized network properties and winner-loser effects do shape dominance hierarchies, but also that specific attributes make individuals more or less susceptible to these effects. The cognitive abilities required to perpetuate these self-organization dynamics are memory and inference [43].

Winner-loser effects reduce the deleterious effects of competition in animal societies [39]. Both winners and losers acquire information in contests about the resource holding power (RHP) of their opponents, even when the contests involve no physical fighting [38]. This new information allows both opponents to make strategic

improvements in subsequent contests. Imperfect information about the relative RHP of group members affects the speed with which linear dominance hierarchies emerge in animal societies; theoretical models suggest that hierarchies form most quickly when information is highly reliable and loser effects are most common [44]. Losers often quickly learn to avoid further direct conflict by altering or inhibiting their behavior in the presence of higher-ranking conspecifics [45, 46].

Mediating mechanisms

Gonadal steroid hormones are well known to affect aggressive behavior. Both organizational and activational effects of androgens enhance aggressiveness in mammals [47, 48, 49]. For instance, intrauterine position affects aggression and dominance in octagon degus via organizational androgen effects [26]. Several neuroendocrine mechanisms have been identified that mediate winner-loser effects on aggressive behavior in invertebrates, fish, mice and humans [40, 16, 50]. Winner effects in invertebrates are mediated by the biogenic amine octopamine [38]. In vertebrates, winner effects appear to be mediated by androgens; acute increases in androgens during contests help prepare the competitor, by activating receptors in the brain that increase the salience of violent threat [51, 16, 52, 53). Evidence regarding proximal mechanisms mediating loser effects is patchier, and varies among species. Among vertebrates, elevated levels of corticosteroids are often detected in losers [38], sometimes in both winner and losers [54], and in several species, depressed plasma androgen levels also accompany defeat [38]. Differences in social rank are often associated with differential sex steroid profiles [55]. Evidence from humans suggests

that both testosterone and cortisol are importantly involved in the mediation of aggression and dominance [56].

The formation of social hierarchies is associated with activation of specific brain regions. The prefrontal cortex (PFC), the amygdala and the serotonergic system have been identified as critical parts of the neural circuitry influencing expression of dominance behavior [57 48, 4]. Excitatory synapses in the medial PFC (mPFC) are stronger in dominant than subordinate mice, and manipulation of synaptic strength in the mPFC changes social status. Winning in contests evidently leads to strengthening of mPFC synapses, whereas losing weakens them. During social confrontations, the mPFC may communicate with the amygdala for emotional processing, with the serotonergic system for motivation to act, and with the striatum for assigning salience [4]. Serotonin (5-HT) inhibits aggression in many species [e.g., 58]. The brainstem dorsal raphe nucleus (DRN) is the main serotonergic nucleus in the vertebrate brain. Studies in mice, monkeys and fish reveal that reduced serotonergic function is associated with increased aggressive behavior [4, 59, 60]. In a socially dominant individual, a stronger mPFC output to the DRN may increase motivation to compete in social conflicts [4].

Work with a cichlid fish (*Astatotilapia burtoni*) sheds light on the neural signaling processes associated with changing dominance status. Differences in 5-HT signaling between dominants and subordinates are mediated, at least in part, by two types of 5-HT receptors in the telencephalon. Serotonergic transmission in the preoptic area also contributes to facilitating the physiological and behavioral changes typical of social descent. On the other hand, the nonapeptide arginine vasotocin (AVT) appears to

regulate social ascent in *A. burtoni* [58]. Individuals ascending in social rank have higher AVT levels and receptor expression than do either stable subordinate or stable dominant animals, indicating a role for AVT during the transition to social dominance, but not its maintenance [58]. AVT may affect behavior by regulating specific motivational systems or specific motor patterns, or it may be involved in determining the salience of aggressive stimuli.

Molecular genetic tools have permitted elucidation of some of the genes involved in the mediation of aggression [e.g., 61] and dominance status [62] in non-human animals. Unsurprisingly, genes associated with many of the neuroendocrine mechanisms discussed above appear to influence aggressive behavior. Epigenetic research has also shed considerable light on the mediation of aggressive behavior; both maternal exposure to stress and early-life adversity affect gene methylation patterns and reduce glucocorticoid receptor density in key brain regions in offspring, which in turn increases their stress reactivity and aggressiveness [e.g., 63; 64]. Adult aggression in rats can also be enhanced by peripubertal administration of corticosteroids, which presumably also affect patterns of gene expression in the brain [65].

Adaptive significance

Aggression functions importantly in group defense [66, 67], and to access critical resources such as food [68, 46, 69], nest sites [70, 71], or mates [72, 73, 74, 75, 76). In some species, males use aggression to overcome female choice [e.g., 73, 10] and thereby enhance their own reproductive success. Thus sexual coercion can function as an adaptive strategy. Aggressiveness as a personality trait can have important effects

on the fitness of the individuals possessing this trait (77). Furthermore, the mixture of aggressive personalities within a social group can have major effects on the growth and persistence of the group. For instance, in the gregarious spider *Anelosimus studiosus*, colonies founded by aggressive individuals grow more slowly than others, but are also far less susceptible to extinction (78). The founders are 'keystone' individuals, which are those having an unusually large effect on group dynamics; the aggressiveness of founders can thus ultimately affect the composition of multispecies communities (79).

Contemporary work has confirmed Schjelderup-Ebbe's [1] hypothesis that stable dominance hierarchies function to reduce intense conflicts and injuries, save energy, and promote social stability. Hierarchy instability induces endocrine and oxidative stress responses [80, 81]. A stable social hierarchy has, in fact, been identified as a fundamental building block of cooperation in animal societies [55]. Unnecessary friction due to conflicts of interest or repeated negotiations of dominance relationships can be avoided if individuals express appropriate behavior for their relative social status. The second building block of cooperation between individuals with conflicting fitness interests is the exertion of social control to prevent cheating [55]. Social rank often needs to be persistently reinforced with aggression emitted by dominants.

Phylogenetic history

The evolution of aggression is shaped by a fitness-optimizing trade-off between its benefits (i.e., securing limited resources) and costs (i.e., risk of injury; loss of time and energy) [82]. Significant work has focused on the phylogenetic emergence, maintenance or loss of specific traits representing both causes and effects of

aggression. Trait simplification and loss are widespread and frequently associated with speciation events. Red throat patches, which represent badges of status, have been lost during evolution of some populations of three-spined sticklebacks, and this loss has affected male-male aggressive behavior in these animals [83]; males that have lost status badges direct more aggression toward males in which these signals have been retained. In another case, this one involving a derived cichlid species, a recent evolutionary shift from non-territorial females to females that defend territories, just as males do, has resulted in the loss of sexual size dimorphism because contest competition for territories selects for large body size in both sexes [84].

Dominance relationships vary considerably among species, from highly despotic and nepotistic to tolerant and egalitarian [85]. It remains unclear whether positions occupied by particular species on this continuum can be best explained by ecological demands or phylogenetic relationships. Primatologists have found considerable support for socio-ecological models [e.g., 86] suggesting that ecological forces shape convergent societies in particular habitat types. However, much of the variation in primate rank relationships cannot be explained by socio-ecological models, so alternative efforts have focused on the possibility that phylogenetic inertia constrains social evolution by limiting animals' responses to specific ecological pressures [e.g., 85]. Indeed, the degree of despotism in societies of multiple clades of primates reveals a strong phylogenetic signal [87, 88, 85]. Clearly, both socioecological and phylogenetic effects must be considered in attempts to explain the evolution of animal societies.

Quantifying dominance relationships

Quantification of dominance relationships permits testing of hypotheses concerning the function of dominance, assessment of the properties of societies that emerge from dyadic interactions, and comparisons among groups; it also enhances our understanding of the role dominance plays in various types of societies (**Figure 1.1**). To date, efforts to quantify, compare, and explain dominance hierarchies have suffered from a lack of consensus on methods and difficulties in dealing with unresolved relationships, which occur when two individuals in a society are never observed to interact [87]. Estimates of hierarchy linearity and steepness decrease with an increasing proportion of unresolved relationships, as does the reliability of rank assignments [87]. Researchers should report the proportion of unresolved relationships in their data, but many do not. Several workers have developed methods for dealing with unresolved relationships [e.g., 89], although the general applicability of these methods remains to be seen.

Advances in social network analysis (SNA) provide versatile new techniques for assigning dominance ranks and quantifying societal properties. These techniques either focus on local substructures of networks ['motif' approaches; e.g., 90, 43] or global network properties [e,g., 91, 92]. Using a network motif approach to understand hierarchy emergence in a newly-formed group of monk parakeets, Hobson & DeDeo [43] found that parakeets directed less aggression toward distant individuals in their aggression sub-network than toward nearby individuals, suggesting that they use transitive inference to infer relative ranks based on observation of agonistic interactions among group-mates. Similarly, Dey & Quinn [92] used Exponential Random Graph

Models to determine that pukeko hierarchies were shaped both by individual attributes and local network substructures. Finally, SNA methods can be used to measure the flow of information through dominance networks, and this information can be critical for coordinated group actions [93]. Pasquaretta et al [94] assessed the efficiency of information flow through networks of 78 groups from 24 primate species, and found that egalitarian networks have more efficient information transfer than despotic ones, suggesting a negative selection pressure on individual aggressiveness or positive selection for tolerance of other individuals. Overall, SNA methods provide a promising platform for unifying approaches to quantifying dominance relationships.



Figure 1.1. Three depictions of a single dominance hierarchy. A multitude of different approaches have been used for quantifying and visualizing dominance hierarchies. a) Interaction matrices tabulate the number of wins and losses sustained by each individual in aggressive interactions during a specified time period, with winners listed in the rows and losers listed in the columns. Optimal rank orders minimize the number of wins listed below the diagonal. b) Glicko and Elo ratings continually update rank scores after each interaction and are useful for studying dynamic aspects of dominance hierarchies such as hierarchy stability. c) SNA methods treat dominance hierarchies as networks, with nodes corresponding to individuals and directional edges depicting the outcomes of conflicts. In this case, more dominant individuals are depicted in darker shades of red. SNA methods allow for the detection of relationships between local and global network properties in determining dominance. Figures reproduced with permission from So et. al [15].

Evolution of human societies

Some fascinating recent work focuses on the evolution of sociopolitical structure in humans. In most primates, aggressive between-group encounters are rare or absent. This is often ascribed to the presence of collective action problems, which emerge whenever collective action creates a public good (e.g., a territory) and the selfish interests of group members are not highly aligned [67]. Analysis of 138 group-living primate species revealed that 45% of species indeed suffer from collective action problems, and indicated that the intensity of between-group competition in primates is more strongly affected by social dilemmas than by ecological conditions. It appears that collective action problems represent an important selective force in the social evolution of group-living primates.

In all multimale-multifemale primate societies except that of *Homo sapiens*, individuals vary in dominance based on motivation and physical prowess, such that dominant individuals gain fitness at the expense of subordinate group-mates [95]. During human evolution, by contrast, persuasion and influence became a new basis for social dominance, allowing for more egalitarian societies than those found in nonhuman primates. Gingtis et al [95] argue that replacement of the ancestral social dominance hierarchy with the more egalitarian sociopolitical structure found in human societies resulted from the combined effects of two factors: development of lethal weapons, which led to the suppression of dominance based on physical prowess, and a marked increase in cooperative activities, such as group hunting of large game, that promoted social interdependence. These conditions favored the emergence of leaders

able to motivate and persuade, and selected for language skills, social agility, and enhanced cognitive abilities.

DISCUSSION

Aggression has long been known to be of central importance in the lives animals, but recent research has allowed development of an interdisciplinary overview of aggression and dominance that spans multiple levels of analysis. Our contemporary view of aggression and dominance is emerging from research in a variety of disciplines, including endocrinology, social network theory, neurobiology, evolutionary biology and behavioral ecology. Early life experiences and other epigenetic effects have profound effects on adult aggressiveness and dominance status, and an individual's aggressive phenotype is mediated by multiple interacting systems in the brain, as well as by circulating concentrations of multiple hormones. Aggressive behavior is important for accessing and defending critical resources and for establishing dominance status. Networks of repeated aggressive interactions in many animal groups yield dominance hierarchies, which function to limit escalated conflict within groups, maintain social stability, and promote cooperation. Evolutionary patterns of aggression and dominance suggest that these traits are constrained by phylogeny, and that changes in these traits may be importantly involved in speciation events. Although the mechanisms that underlie formation of dominance hierarchies remain poorly understood, social network analysis and other methodological advances provide promising avenues for future research.

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CHAPTER TWO

INFERRING LONGITUDINAL HIERARCHIES: FRAMEWORK AND METHODS FOR STUDYING THE DYNAMICS OF DOMINANCE

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ABSTRACT

Social inequality is a consistent feature of animal societies, often manifesting as dominance hierarchies, in which each individual is characterized by a dominance rank denoting its place in the network of competitive relationships among group-members. Most studies treat dominance hierarchies as static entities despite their true longitudinal, and sometimes highly dynamic, nature. To guide study of the dynamics of dominance, we propose the concept of a longitudinal hierarchy: the characterization of a single, latent hierarchy and it's dynamics over time. Longitudinal hierarchies describe the hierarchy position (r) and dynamics (Δ) associated with each individual as a property of its interaction data, the periods into which these data are divided based on a period delineation rule (p), and the method chosen to infer the hierarchy. Hierarchy dynamics result from both active (Δa) and passive (Δp) processes. Methods that infer longitudinal hierarchies should optimize accuracy of rank dynamics as well as of the rank orders themselves, but no studies have yet evaluated the accuracy with which different methods infer hierarchy dynamics. We modify three popular ranking approaches to make them better suited for inferring longitudinal hierarchies. Our three 'informed'

methods assign ranks that are informed by data from the prior period rather than calculating ranks *de novo* in each observation period, and use prior knowledge of dominance correlates to inform placement of new individuals in the hierarchy. These methods are provided in an R package. Using both a simulated dataset and a long-term empirical dataset from a species with two distinct sex-based dominance structures, we compare the performance of these methods and their unmodified counterparts. We show that choice of method has dramatic impacts on inference of hierarchy dynamics via differences in estimates of Δa . Methods that calculate ranks *de novo* in each period overestimate hierarchy dynamics, but incorporation of prior information leads to more accurately inferred Δa . Of the modified methods, Informed MatReorder infers the most conservative estimates of hierarchy dynamics and Informed Elo infers the most dynamic hierarchies. This work provides crucially needed conceptual framing and methodological validation for studying social dominance and its dynamics.

INTRODUCTION

Social inequality is a surprisingly consistent feature of group living. This inequality often manifests as a dominance hierarchy, in which repeated agonistic interactions between group members lead to the emergence of a linear order of individuals from high to low rank [1], with rank position often determining priority of access to resources. Found in a diverse set of organisms including protists [2], insects [3], fish [4], mammals [5], and birds [6], dominance hierarchies promote group stability and reduce the costs of living in an uncertain social environment [7,8]. Since the first

description of a 'peck order' among chickens [6], dominance hierarchies have proven to be an important force structuring myriad aspects of an organism's biology, including its space use [9,10], health (Sapolsky 2005; Flies et al. 2016; Snyder-Mackler et al. 2016), longevity [14,15], and reproductive success [16,17].

Dominance hierarchies are dynamic systems: the positions of individuals within a hierarchy can change over time due to temporal variation in demography, ecological conditions, ontogenetic development, or the relative body condition of group members [11,18–20]. Nevertheless, most studies treat dominance as a constant individual attribute rather than a transient state. This static approach to dominance is appropriate for many studies conducted over short periods of time; consistency, at least over short time-scales, is a defining feature of dominance relationships [21]. Although useful for understanding the consequences of dominance hierarchies, this approach does not allow for the study of system dynamics. Understanding these dynamics will facilitate study of the structure of inequality in animal societies, the relationships between dominance networks and other social networks, and the stability of dominance hierarchies. The rapid recent advances in social network analysis techniques [22-24] offer promising means for incorporating dominance hierarchies into the more general study of dynamic social networks, but reliable inference of hierarchies and their dynamics is a requisite first step.

Until now, an explicit framework for investigating the dynamics of dominance hierarchies has been lacking. Most studies estimate the dynamics of dominance systems by dividing the study into periods, determining ranks independently within each period, and inferring changes in rank based on the differences observed between one

period and the next [18,19,25–29]. Others simply report directly observing changes [30– 32]. Most studies focus on rank reversals, in which one or more dyads reverse their dominance relationship, often in association with agonistic interactions, including "revolutionary challenges." Some workers only identify rank reversals if the reversals are observed to be persistent [18,33], but it is often unclear whether or not transient cases are included as rank reversals. The Elo-rating [34-36] method provides an alternative approach to studying the dynamics of dominance; here, numerical dominance scores for individuals are calculated by progressively updating previous scores. Application of the Elo-rating method to identify the dynamics of dominance also varies. Changes in the social hierarchy are sometimes inferred based on absolute changes in an individual's score [35], and in other cases inferred from changes in the ordinal positions of individuals (i.e., changes in ordinal rank rather than score; [35,37]). Furthermore, changes in the social hierarchy are assessed after varying time periods such as after each new interaction [38,39], after longer time periods [35], or in discreet periods before and after a salient event [13,37,40]. Finally, dominance hierarchy dynamics can result from demographic processes (e.g., birth, immigration) and relational processes (i.e., reversal of previous dominance relationship), but clear distinction between these two types of dynamics is currently lacking. In light of these varied approaches, it would be useful to have an explicit framework for assessing the dynamics of dominance hierarchies.

Here we advance the 'longitudinal hierarchy framework,' an explicit approach to estimating the dynamics of dominance hierarchies. The focus of this framework is on identifying the foundational concepts in the dynamics of dominance. Next, we identify

incorporation of new individuals and accurate estimation of hierarchy dynamics as two primary challenges to inferring longitudinal hierarchies, and propose solutions to both challenges. We then incorporate our solutions into three widely-used approaches to inferring dominance hierarchies: Matrix reordering, Elo-rating, and David's Scores. Matrix reordering, of which the I&SI method [1] is the most commonly used, produces rank orders by iteratively rearranging the order of individuals to maximize the fit to the observed interaction data. Elo-rating [34,36] and David's Score [41,42], on the other hand, calculate numerical dominance scores based on the interaction data. Our extended versions of these methods are provided in a new, user-friendly R package called DynaRankR [43]. Finally, we use both simulated and empirical data from a longterm field study of spotted hyenas (Crocuta crocuta) to assess the performance of the modified and un-modified methods in inferring longitudinal hierarchies. Our results indicate that the modified methods outperform their unmodified counterparts, and that the three improved methods are all viable, with each having distinct, situation-specific advantages. We hope that the longitudinal hierarchy framework and the methodological advances we present here will encourage future research on the structure and dynamics of non-egalitarian societies.

Longitudinal hierarchy framework

To guide research on the dynamics of dominance, we propose the concept of a 'longitudinal hierarchy', which is the characterization of a single, latent hierarchy within a social group and it's dynamics over time (**Figure 2.1**). In this framework, a longitudinal hierarchy describes the hierarchy position (*r*) and dynamics (Δ) associated with each

individual as a property of the interaction data, the periods into which these data are divided based on a period delineation rule (*p*), and method used to estimate the hierarchy. Here, we describe this framework and the details of *p*, *r*, and Δ .



Figure 2.1. A longitudinal hierarchy characterizes not only the rank orders observed at specific time points, but also the dynamics of a single latent hierarchy over time. That is, in addition to the rank orders observed at specific time points, a longitudinal hierarchy includes the changes in rank occurring between observation time points. Letter subscripts refer to individual identities and number subscripts refer to time period.

To infer a longitudinal hierarchy, the total length of the study is first divided into periods as determined by p, the period subdivision rule. This rule could be a unit of time (e.g., daily, yearly), or it could be determined by biologically relevant events (e.g., breeding cycles, rainy seasons, etc.). Application of this rule results in a sequence of individual time periods (t) spanning the whole study; depending on choice of p, each period could be long enough to encompass many interactions or shortened to contain only one interaction (i.e., progressively updating ranks after each interaction). Although any period delineation approach is consistent with the longitudinal hierarchy framework,

some approaches are likely to work better than others depending on the ranking method used, data availability, and the biology of the study organism. Furthermore, studies that aim to relate the structure or dynamics of a longitudinal hierarchy to some other variables of interest should consider these other variables in selection of *p*. For example, a study aiming to relate resource availability to hierarchy dynamics should delineate periods with a length appropriate for measuring resource availability.

After dividing the full dataset into periods, a ranking method of choice is applied to the data from each period to infer dominance values (*r*) for each individual (*i*) in each period (*t*). These dominance values (r_{i,t}, r_{i,t+1}, etc.) could be either cardinal scores for methods that assign numerical rank scores (e.g., Elo-rating, David's Scores), or rank orders, depending upon the research question. Numerical scores are statistically convenient and are more useful for addressing some research questions than is a simple rank order [35,36]. However, as we discuss in the next section, we recommend use of rank orders wherever possible because they allow more precise interpretations of hierarchy dynamics.

The final step in inferring a longitudinal hierarchy is to calculate hierarchy dynamics (Δ) for each individual (*i*) after each period (*t*). These dynamics are simply calculated as

$$\Delta_{i,t} = r_{i,t} - r_{i,t-1}$$

or the difference between each individual's dominance value in the current and previous periods. For clarity, Δ_t corresponds to dynamics between period *t-1* and *t*, and Δ is signed such that negative values indicate downward movement and positive values indicate upward movement. Dominance dynamics for any single individual $\Delta_{i,t}$ comprise

the sum of its changes due to active processes ($\Delta a_{i,t}$) plus changes due to passive processes ($\Delta p_{i,t}$). Active processes include changes in dominance relationships associated with changes in patterns of outcomes of contests among individuals present in the study population during consecutive time periods. For instance, if in period *t-1* animal A consistently beats B in contests (and thus has a superior dominance value to B), but B consistently beats A in period *t* (and thus has a superior dominance value to A), these two individuals are considered to have reversed their previous dominance relationship and to have Δa_t values of -1 (down the hierarchy) and 1 (up the hierarchy), respectively. The equation for calculating $\Delta a_{i,t}$ is

$$\Delta a_{i,t} = (|\boldsymbol{D}\boldsymbol{o}\boldsymbol{m}_{i,t}| - |\boldsymbol{D}\boldsymbol{o}\boldsymbol{m}_{i,t-1}|)$$

where
$$Dom \subseteq (r_t \cap r_{t-1})$$

where $|Dom_{i,t}|$ is the cardinality (i.e., # of individuals) in the set of individuals that *i* is able to dominate during period *t*, and *Dom* is limited to only those individuals present in the rank orders in both periods *t* and *t-1*.

In contrast to active processes, change due to passive processes ($\Delta p_{i,t}$) occurs in the absence of changes in patterns of contest outcomes. Passive processes include demographic events like births, deaths, immigration and emigration. For example, if individual B is the second-most dominant in the group and individual A, the most dominant, dies, individual B moves up one position due to passive processes ($\Delta p_t = 1$). $\Delta p_{i,t}$ is calculated as [the number of individuals that dominated *i* in period *t*-1 that are no longer present in the group during period *t* (i.e., dominant individuals who died or left the group)] minus [the number of individuals that dominate individual *i* during period *t* that were not present in period *t*-1 (i.e., new individuals who dominate *i*)]. More simply, $\Delta p_{i,t}$ can be calculated as $\Delta_{i,t} - \Delta a_{i,t}$, because total dominance dynamics Δ_{it} result from the sum of these two processes. As an example, consider individual X, who is observed consistently dominating three individuals who were previously higher-ranking than X, but exhibits appeasement behavior to a new individual, Y, who has recently immigrated into the group and dominates X. Individual X thus has $\Delta a_t = 3$ and $\Delta p_t = -1$ for a total $\Delta_t = 2$.

The type of dominance value (i.e., numerical scores, rank order) assigned by the ordering method influences the calculation of Δ . In the previous examples, we considered the dominance value to be a rank order, and the unit of Δ is number of rank positions. Although the theory outlined above still holds for numerical scores, the means of calculating Δ and its components differ. For numerical scores, it is easy to calculate Δ , but interpreting the value of Δ is less straightforward. Numerical scores calculated by David's Score are influenced by the number of individuals in the group [44], and Elorating scores change with each new observed interaction [35], even if the interaction merely reinforces the status quo. Thus, for example, a $\Delta_{i,t}$ of 20 could be interpreted as either a dramatic or an insignificant change, depending on the circumstances. Furthermore, it is not clear how a numerical Δ can be decomposed into Δa and Δp , because individuals influence each other's scores indirectly via the scores of other group members. For these reasons, we believe that ordinal rankings are better than numerical scores for identifying hierarchy dynamics, and recommend their use in the absence of strong motivation for using numerical scores. As such, we will use rank as representative of individual dominance value throughout the remainder of this paper.

After running Elo-rating and David's Score algorithms, we extract rank orders from the numerical scores.

In sum, a longitudinal hierarchy describes both ranks (*r*) and rank dynamics (Δ) of each individual in a social group over time as a function of a period delineation rule (*p*), the interaction data, and the ranking method used to determine *r*. Rank dynamics, including both active processes (Δa) and passive processes (Δp), are calculated as the difference in ranks held by individuals in successive periods. Thus, for clarity and reproducibility, when inferring a longitudinal hierarchy, researchers should report *p*, the ranking method used, and a summary of the data, and should articulate whether the dynamics of interest in their study are Δa , Δp , or Δ . In the remainder of this paper, we discuss the choice of ranking method for inferring longitudinal hierarchies.

Ranking methods for inferring longitudinal hierarchies

The optimal method for inferring longitudinal hierarchies will maximize the accuracy of both *r* and Δ . Ranking methods have been well studied in their ability to estimate *r* [45,46], but no studies have yet evaluated the accuracy with which different methods infer Δ . In light of these two optimality criteria, we identify two primary methodological challenges to inferring longitudinal hierarchies, and recommend some solutions. We then propose modifications that incorporate these solutions into three popular ranking approaches: matrix reordering (I&SI), Elo-rating, and David's Score.

Although Δ is calculated directly from *r*, accurate estimates of *r* do not necessarily produce accurate estimates of Δ . In particular, it is easy for methods to overestimate Δ_t if r_t and r_{t-1} are inferred independently, because slight inaccuracies in the rank orders

calculated during each period suggest active dynamics that never took place (**Figure 2.2**). In light of limited sample size, sampling error, and natural variation in the outcome of dominance interactions, the problem is how best to discriminate between constant and shifting dominance ranks. We propose that an optimal procedure for inferring a longitudinal hierarchy allows ranks at time period *t* to be informed by the ranks from period *t-1* such that individuals tend to maintain their ranks over time unless interaction data suggest otherwise. This 'inertial tendency' is justified by the very definition of dominance, which includes temporal stability as an essential component [21], and the notion that dominance hierarchies reduce uncertainty about the outcomes of contests between group members [7,8] assumes that the state of the hierarchy at a given time is predictive of future interactions. The Elo-rating method [35,36] implements this 'inertial tendency' by updating dominance scores after each interaction, making it well suited for inferring longitudinal hierarchies.



Figure 2.2 The true state of the hierarchy (a) and an imperfect longitudinal hierarchy estimating it (b). Rank orders in (b) have a Pearson's rank correlation with the true orders of 0.9. The longitudinal hierarchy in (b) overestimates the dynamics in the hierarchy as a result of small inaccuracies in rank orders at both t1 and t2. Letter subscripts refer to individual identities and number subscripts refer to time period.

The incorporation of demographic changes poses another critical challenge to inferring accurate longitudinal dominance hierarchies. Although individuals leaving the group (due to emigration or death) don't pose a major problem, individuals who join the group (due to immigration or birth) need to be included in the hierarchy in appropriate places. One approach is to have individual-specific 'burn-in' periods, where some early data for each new individual are used to assign its starting rank, and that individual is then added to the hierarchy at the end of the burn-in period. This burn-in paradigm is used on the whole hierarchy in the Elo-rating method, and can result in significant amounts of discarded data, which is particularly troubling when interaction data are sparse [38]. A better approach uses prior knowledge of dominance correlates to inform the placement of new individuals in an existing hierarchy. The success of this approach

will vary among species, and it will only be viable for species for which prior research has identified one or more reliable correlates of dominance rank. For example, an individual joining a group in a species where rank has previously been found to be positively correlated with body size is added to the hierarchy according to its body size relative to other members of the group; if it is now 10th largest in the group, it would be assigned a rank of 10. Subsequently, this individual's position is updated based on observations from that period, such that its final position for the first period in which it appears in the hierarchy is reflective of a combination of the dominance correlate and the observed interactions from that period. Newton-Fisher (2017) [38] used prior information about individual dominance ranks to improve the effectiveness of the Elorating method in resolving a hierarchy of male chimpanzees. Not only does this approach eliminate data lost from a burn-in period, but it also allows for systematic study of the causes of deviation from expected rank based on rank correlates. Here, we take a similar approach to Newton-Fisher (2017) by adding new individuals to the hierarchy based on prior information.

We propose modified versions of matrix reordering, Elo-rating, and David's Score ranking approaches that incorporate both information about prior ranks and dominance correlates into hierarchy inference. The modified methods infer *r* for each period <u>informed</u> by the previous periods, and new individuals are incorporated into the longitudinal hierarchy in a manner <u>informed</u> by prior knowledge of dominance correlates; thus, we name these modified methods Informed MatReorder, Informed Elo, and Informed David's Scores (**Table 2.1**). Each modified method is introduced below.

Matrix reordering

The I&SI matrix-reordering algorithm rearranges a rank order to minimize first the number of inconsistencies (dyads for which the most common outcome of interactions is inconsistent with the rank order), and second the strength of inconsistencies (the difference in rank between members of a dyad involved in each inconsistency) [1,47]. When applied in the longitudinal hierarchy framework, this approach infers rank orders independently for each period.

The Informed MatReorder method is a modified version of I&SI that minimizes both the number of inconsistencies and the difference between rank orders in successive periods. Crucially, whereas I&SI attempts to reorder every individual in each period, Informed MatReorder only moves individuals involved in inconsistencies in the current period. New individuals are added to the order according to prior knowledge of dominance correlates, and before the reordering process. Individuals involved in an inconsistency are then moved to other positions to resolve the inconsistency, and this process is repeated iteratively. When this procedure identifies multiple orders with the fewest inconsistencies, the optimal order is selected as the order with fewest inconsistencies that is also most similar to the order from the previous period (See Appendix A: Informed MatReorder method description for more details on these steps). Informed MatReorder also includes an optional validation rule, which allows inconsistencies to be ignored if there are no subsequent observations of the dyad that corroborate the inconsistency. A transiently inconsistent outcome in a dyadic fight might occur, for example, when a low-ranking female defends her offspring against a higher-ranking female; the apparent reversal in the rank relationship between the two

adult females indicated by their agonistic behavior does not necessarily persist after the specific fight in question. This approach is similar to that taken by other researchers (e.g., [18]). Because future observations are required to corroborate any observed inconsistency, studies using the optional validation rule should exclude the final period from their analysis, as no subsequent observations are available for that period.

Elo-rating

The Elo-rating method is a points-based data-stream approach where the scores of two interacting individuals are updated after each interaction based on the outcome of the interaction. Winners gain points and losers lose points proportional to the difference between their scores before the interaction, scaled by some constant K [35,36]. In the longitudinal hierarchy framework, scores are updated after each interaction and ranks are determined by the scores of individuals at the end of each period. Because new data update previous scores, the standard Elo-rating procedure already incorporates the 'inertial tendency' we identify as necessary to prevent overestimation of Δa . However, in the standard Elo-rating approach, new individuals are added to the hierarchy with an arbitrary score (here we use mean of scores of other group-mates). In the Informed Elo method, new individuals enter the hierarchy with a score informed by their previously identified dominance correlate, with an Elo score set to the mean of the two individuals adjacent to it in the hierarchy. In both Informed Elo and standard Elo-rating, we use K = 100, following earlier workers [35,48]. However, we also tested K = 200, but this had no effect on the conclusions of the study (Appendix E: Simulation results with Elo parameter K=200).

David's Score

The David's Score method is a points-based approach in which an individual's score is determined by the number of individuals it dominates, weighted by the ability of each of those individuals to dominate other members of the group [42]. As recommended by others [44], we use the D_{ij} index to calculate David's Scores, which accounts for the number of interactions observed within each dyad. The equation for D_{ij} is

$$D_{ij} = P_{ij} - \frac{P_{ij} - 0.5}{n_{ii} + 1}$$

where P_{ij} is the proportion of interactions in which *i* wins over *j*, and n_{ij} is the number of interactions observed between *i* and *j*. The fraction that is subtracted from P_{ij} can be interpreted as (observed proportion wins – expected proportion wins) ÷ (probability of observed proportion wins) [44]. Scores for each individual are calculated according to the formula

$$DS = (w + w_2) - (l + l_2)$$

where *w* is the sum of D_{ij} values for each individual *i*, I is the sum of D_{ji} values for individual i, and *w*2 and *l*2 are the *w* and *l* values weighted by the *w* and *l* values of interaction partners [42]. In the longitudinal hierarchy framework, standard David's Scores are calculated independently for each period. In Informed David's Scores, D_{ij} values from previous periods are used to calculate the D_{ij} for the current period. In this modified method, the formula for D_{ij} in period *t* is:

$$D_{ij,t} = P_{ij} - \frac{P_{ij} - D_{ij,t-1}}{n_{ij} + 1}$$

This modification follows naturally from the definition of the original equation; in the original equation, the 'expected proportions of wins' was set to 0.5; in the modified version, the expected proportions of wins is set to the D_{ij} from the previous period. Thus, D_{ij} for the current period reflects D_{ij} from the previous period, updated by data from the current period. New individuals are added to the hierarchy according to the dominance correlate. Starting D_{ij} values for new individuals are set to the values they would have if they had been observed losing once to all higher ranked (according to dominance correlate) individuals. If a dyad is not observed interacting in a study period, their D_{ij} for that period is equal to their D_{ij} from the previous period.

The Informed MatReorder, Informed Elo, and Informed David's Scores methods are adaptations of existing methods that use prior knowledge of dominance correlates to place new individuals in a hierarchy, and infer *r* for each period by updating the ranks (or scores) from the previous period (see **Table 2.1** for a concise summary of the modifications). The use of information from the previous period necessitates special treatment of the first period, because there is no previous period to use. To serve as the 'previous order' for the first period, the user must supply an 'initial order' to the informed ranking methods in DynaRankR. This initial order might be determined by the dominance correlate used in the study, an order generated by a different ranking method, or some other well-justified choice of initial order. The initial order is used by each informed method to serve as a stand-in for the period prior to the first (like a '0th' period) when determining the order for the first period. In Informed MatReorder, this initial order serves as the basis for the second reordering optimization criterion (new

order is minimally different from previous order). In Informed Elo, initial scores for the first period are set to K * (rank according to initial order - 1) before being updated by the observations from the first period. With David's Score, each dyad starts with the D_{ij} they would have received if they had interacted once and the winner was determined according to the initial order, and these D_{ij} values are used as D_{i,j,t-1} when calculating David's Scores for the first period. In sum, for each of these methods, the order in first period is determined by modifying the initial order with the interaction data during the first period.

To assess the efficacy of the modified and unmodified methods at inferring longitudinal hierarchies, we compared the performance of these methods on simulated and empirical hierarchies.

Original	Modified
I&SI : Reorders interaction matrix iteratively to minimize (1) number of inconsistencies and (2) <u>strength of inconsistencies.</u>	Informed MatReorder : Reorders interaction matrix iteratively to minimize (1) number of inconsistencies and (2) difference from order in previous period. New individuals are added according to prior knowledge of dominance correlates.
Elo-rating: Scores are updated after each interaction depending on outcome. <u>New individuals start with arbitrary score.</u>	Informed Elo: Scores are updated after each interaction depending on outcome. New individuals start with score informed by prior knowledge of dominance correlates.
David's Score : Scores are calculated from dyadic dominance indices, which are calculated as the proportion of outcomes within a dyad in favor of the focal individual, adjusted by the number of observations and the expected proportion of outcomes in favor of the focal individual (0.5).	Informed David's Score: Scores are calculated from dyadic dominance indices, which are calculated as the proportion of outcomes within a dyad in favor of the focal individual, adjusted by the number of observations and the expected proportion of outcomes in favor of the focal individual (D _{ii} from previous period). New individuals start with dominance indices informed by prior knowledge of dominance correlates.

Table 2.1. Summary of the differences between the original ranking methods and their modified counterparts. Differences between the corresponding methods are underlined

METHODS

Implementation of ranking methods

All ranking methods except I&SI were implemented in DynaRankR [43], a new R package for inferring longitudinal hierarchies. I&SI was implemented in the EloRating package [49]. Hierarchy dynamics were calculated from rank orders generated by each of these methods using the get_dynamics function in the DynaRankR package.

Simulated data

To compare performance among these methods in a situation with a known true hierarchy, we simulated 10 longitudinal hierarchies, each comprised of 20 individuals and spanning 20 study periods. We simulated Δa by randomly selecting individuals to change positions in the hierarchy, and we generated hierarchies with moderate numbers of changes of small magnitude, and others with many changes of large magnitude, to assess the performance of each method under varying conditions. In each study period, the number of individuals undergoing changes was randomly selected from a Poisson distribution (lambda = {1, 5}). The number of rank positions each individual moved up or down the hierarchy during a rank change was drawn from an exponential distribution (rate = {1, 0.5}), and a random sample from a binomial distribution (prob = {0.5, 0.5}) determined whether they moved up or down. Additionally, we simulated Δp by including a 20% probability that a new individual would enter the hierarchy at a random location in each study period and a 20% probability that a random set of a study period.

Simulated interactions were generated using the generate_interactions function in the aniDom package [50], with parameters a = 15 and b = 0, both ID- and rank-based biases, and generating 20 interactions per individual. This produced hierarchies similar to those found in gregarious vertebrates, in which (1) higher-ranked individuals were very likely to win interactions, (2) this likelihood increased with the rank difference between the two individuals, and (3) individuals varied with respect to the number of interactions in which they engaged (see Farine & Sanchez-Tojar, 2017; Sánchez-Tójar, Schroeder, & Farine, 2017 for details). Because ranking methods are highly sensitive to the proportion of 'unknown' dyads, or dyads for which there are no observed behavioral interactions during the study period [1,35,42,51], we tested each method with three different proportions of missing data. Henceforth we will refer to this proportion as "% unknowns", following Klass & Cords (2011). To do this, we removed observations from randomly selected dyads until the % unknowns matched a predetermined value, which we set to low (20%), medium (50%) or high (80%). The simulation occasionally produced more than 20 % unknowns before any data were removed, in which case we simply left all data intact in the 'low' condition. For the methods incorporating prior knowledge of dominance correlates, we simulated an arbitrary dominance correlate (e.g., body size) value between 0 and 100 for each individual such that the Spearman's rank correlation between the trait value and the true ranks matched a specified value, which we set at 0.9, 0.7, 0.5, and 0.2 (see Appendix B: Simulation results with less informative dominance correlate). This rank-correlated trait was used as the initial order for all informed methods, and was also used to place new individuals in the hierarchy with these methods.

We assessed the accuracy with which each method inferred rank orders and dynamics using the simulated data. To assess the performance of each method at identifying rank orders, we tabulated the number of dyadic relationships identified correctly and incorrectly by each method across study periods. We used a binomial GLMM to test the effect of ranking method on the proportion of dyads correctly identified; the model included fixed effects of method and % unknowns, and random effects for simulation run and study period nested within simulation run. To assess the accuracy with which each method inferred hierarchy dynamics, we calculated the total magnitude of Δa and Δp each individual experienced in the hierarchies inferred by the different methods and in the true order. We used a Poisson GLMM to test the effect of method on Δa , and Δp ; the model included fixed effects for method and % unknowns, and random effects for simulation run and individual identity nested within simulation run. Because Informed MatReorder uses future observations to corroborate changes observed in any given study period, we excluded the last period from each of our analyses. The first period was excluded from the analysis of each type of Δ because no change in rank is possible.

Empirical data

We tested the performance of the six ranking methods on 27-years of interaction data from a single group of female spotted hyenas. As in many cercopithecine primates, rank acquisition by female spotted hyenas typically follows a pattern of maternal rank inheritance with youngest ascendancy [52,53], wherein each new female acquires the rank immediately below that of her mother but above those of her older sisters. We

used this principal of maternal rank inheritance to add new females to the hierarchies in the informed methods. We conducted a parallel analysis of a corresponding 27-year dataset on immigrant male hierarchies, which are structured by tenure in the social group rather than by maternal rank inheritance [54]. The description of the results of this analysis of male hierarchies appear in *Appendix C: Analysis of the immigrant male hierarchy*; this extra analysis demonstrates the applicability of these methods to societies with different dominance correlates.

The empirical data were collected by personnel of the Mara Hyena Project in the Masai Mara National Reserve in southern Kenya [55] from 1989 to 2015. Contest outcomes were recorded using all-occurrence sampling [56] of agonistic interactions observed during daily morning and evening observation sessions, and genealogical relationships between mothers and daughters were inferred based on genotyping and observations of nursing behavior. Individuals were identified based on their unique spots. We divided the longitudinal datasets into calendar year-long periods stretching from 1988 to 2015; given that hyenas breed throughout the year, calendar year represents a fair but arbitrary break point. Average group size was 24.23 (16-52) adult females, and there were on average 4.6 (1-14) females recruited per year and 3.56 (0-13) females lost per year. We calculated ranks for all females at least 1.5 years old at the start of each year. The 1.5 year age threshold was selected based on previous work indicating that the process of rank acquisition among maturing females is complete at around 1.5 years of age [57]. For the three informed methods, ranks for the first study year were set according to observations made by L.G Frank using a strategy similar to that described by Martin & Bateson 1993 [55]. Triangle transitivity (t_{tri}; Shizuka &

McDonald, 2012) for each year of observations was high (mean = 0.96), and we observed an average of 11.35 interactions per female per year (1.44-27.21), leading to a mean *% unknowns* per year of 66.52 (range 42.39-84.17). Although these values are different from what were depicted in a previous study from the same population [60], the adjacency matrix depicted earlier was created from three years of interactions, whereas the current study separated interactions by year.

We assessed performance of each method based on three criteria: (1) the number of rank changes identified by each method, (2) the proportion of outcomes observed during a particular year that were consistent with the order produced by the method, and (3) the proportion of outcomes observed during the following year that were consistent with the order produced by the method. Based on reports in the literature about the societies of spotted hyenas and other species with maternal rank inheritance, we expect the hierarchy to be highly stable [53–55,61]. Consequently, methods that produce orders that change frequently from year to year (i.e., large Δ) and that are inconsistent with future data are likely to suffer from overfitting. To test the amount of change from year to year estimated by each method, we tabulated the total magnitude of Δa and Δp for each individual identified by each method. We used a Poisson GLMM to test the effect of method on the dynamics identified for each individual; the model included a fixed effect for method and a random effect for individual identity. To test the fit of the orders with the data, we recorded (1) the proportion of aggressive interactions from the current year that were consistent with the order generated for the current year and (2) the proportion of aggressive interactions from the subsequent year that were consistent with the order generated for the current

year. Here we used a binomial GLM to test the relationship between ranking method and the proportion of data consistent with the rank orders produced. In all analyses we used Tukey post-hoc tests (R package *multicomp*, Bretz et al. 2016) to investigate pairwise differences between specific methods.

RESULTS

Simulated data

Both % *unknowns* and ranking method had effects on the accuracy of orders produced (**Figures 2.3a,b**, **2.4a,b**) and on the estimated dynamics in the simulated dataset (**Figures 2.3d,e**, **2.4d,e**). As the % *unknowns* increased, all six methods estimated longitudinal hierarchies with more dynamics due to active processes (simulated hierarchies with few changes: $\beta = 0.415$, p < 0.0001; simulated hierarchies with many changes: $\beta = 0.199$, p < 0.0001) and less accurate rank orders (simulated hierarchies with few changes: $\beta = -2.456$, p < 0.0001; simulated hierarchies with many changes: $\beta = -2.287$, p < 0.0001). The differences in accuracy of *r* were relatively small among most methods, but the informed methods generally estimated *r* with greater accuracy than did their uninformed counterparts (**Figures 2.3a,b**, **2.4a,b**).

Although differences in the accuracy of *r* estimates were small, the methods differed importantly in the accuracy of their estimates of Δ . When tested on fairly stable simulated hierarchies, all methods overestimated Δa , but the informed methods were consistently more accurate than their uninformed counterparts (**Figure 2.3c,d**); Informed MatReorder produced the most accurate estimates of Δa when hierarchies

were fairly stable (Figure 2.3c,d). When tested on highly unstable simulated hierarchies, the Informed David's Score method yielded the most accurate estimate of Δa , Informed MatReorder underestimated Δa , and Informed Elo overestimated Δa (Figure 2.4c,d). In both cases, methods that incorporated an inertial tendency estimated Δa most accurately, whereas methods without an inertial tendency consistently overestimated the dynamics of the latent hierarchy. This is most evident when comparing the unmodified Elo-rating method (which incorporates inertial tendency) to the I&SI and unmodified David's Score; in all studies, the unmodified Elorating inferred far less dynamic hierarchies than did the other two unmodified methods. There were no effects of method or % *unknowns* on Δp (**Figure 2.F.1**). Finally, reducing the informative value of the dominance correlate (by reducing its correlation with the true order from 0.9 to 0.7, 0.5 and 0.2) somewhat reduced the performance of the methods using this information, but did not qualitatively change the pattern of results (Figures 2.B.1, 2.B.2, 2.B.3), suggesting that the informed methods are robust to variation in the accuracy of the dominance correlate.



Figure 2.3. Assessment of ranking methods using a <u>mildly dynamic</u> simulated latent hierarchy. Hierarchies were assessed under conditions of low (20%) medium (50%) and high (80%) proportions of missing data. a) Accuracy of methods, assessed as the proportion of dyadic relationships correctly identified during each period and b) parameter estimates and confidence intervals for the effects of each method, with Informed MatReorder as the reference level (dashed line). All differences among methods were statistically significant except for the difference between Informed Elo and Elo. c) Total magnitude of position changes due to active processes each individual underwent in the hierarchy inferred by the different methods and in the real simulated hierarchy. d) Parameter estimates and confidence intervals for the amount of change identified compared to the amount of change in the true hierarchy (dashed line). All differences among methods were statistically significant. e) Example of one of the 10 simulated hierarchies used in this analysis. Note that confidence intervals are narrow for parameter estimates because of the large sample size.



Figure 2.4. Assessment of ranking methods using a <u>highly dynamic</u> simulated latent hierarchy. Hierarchies were assessed under conditions of low (20%) medium (50%) and high (80%) proportions of missing data. a) Accuracy of methods, assessed as the proportion of dyadic relationships correctly identified during each period and b) parameter estimates and confidence intervals for the effects of each method, with Informed MatReorder as the reference level (dashed line). All differences among methods were statistically significant. c) Total magnitude of position changes due to active processes each individual underwent in the hierarchy inferred by the different methods and in the real simulated hierarchy. d) Parameter estimates and confidence intervals for the amount of change identified compared to the amount of change in the true hierarchy (dashed line). All differences among methods were statistically significant except for the difference between Informed David's Score and the true hierarchy. e) Example of one of the 10 simulated hierarchies used in this analysis. Note that confidence intervals are narrow for parameter estimates because of the large sample size.

Empirical data

In tests with the empirical dataset on philopatric female hyenas, method had strong effects on both Δa (Figures 2.5, 2.6) and on the fit between the identified orders and the observed data (Figure 2.7). Pairwise comparisons (Appendix D: Pairwise comparisons for analysis of female hyena data) revealed that Informed MatReorder produced hierarchies with the fewest Δa per individual (Figure 2.6; p < 0.0001), and all informed methods identified fewer changes than their uninformed counterparts (Figure **2.6**; p < 0.0001). Again, method had no effect on Δp (Figure 2.F.2). Furthermore, although all methods produced orders that were highly consistent with the observations for the current year (Figure 2.7a; Table 2.D.2), the uninformed methods produced orders that were poorly predictive of the outcome of observations from the following year (Figure 2.7b; Table 2.D.3), and changed frequently from year to year (Figure 2.6; Table 2.D.1). Informed MatReorder produced orders that were consistent with the current data, most consistent with future data (Figure 2.7; p < 0.0001), and identified the fewest changes (Figure 2.6). As in the simulation study, methods that incorporated inertial tendency estimated significantly fewer rank-reversals than did methods without inertial tendency. Although we don't know the true number of rank-reversals taking place in the latent hyena hierarchies, the methods that incorporated inertial tendency identified more biologically plausible hierarchy dynamics (Figure 2.5). Finally, despite the fact that male and female hierarchies in spotted hyena clans are organized based on entirely different conventions (tenure in the group and maternal rank inheritance, respectively), results from the immigrant male data corroborated our findings from females (Appendix C: Analysis of the immigrant male hierarchy).



Figure 2.5. (a-f) Visual depiction of the dominance hierarchies identified by each method from the 27-year empirical dataset from a wild population of philopatric female spotted hyenas. Each line represents the rank assigned to a single adult female over the course of her lifetime. Crossing lines indicate an identified reversal of a previously held dominance relationship (i.e., Δa), whereas non-crossing lines indicate stability from year to year in the identified longitudinal hierarchy. Numbers of rank positions varied with number of females present in the group over time.


Figure 2.6. Hierarchy dynamics identified by each method in the empirical dataset from female spotted hyenas. Each boxplot depicts the distribution of the number of positions each individual moved due to active processes over the course of its time in the study.



Figure 2.7. The proportion of observed outcomes of agonistic interactions between philopatric adult female spotted hyenas and the rank orders identified by each method. Data from (a) were from a current year in the study and were used to produce the order. Data in (b) were from the following study year. Disparities between the fit in (a) and (b) indicate overfitting. Letters indicate significantly different groups.

DISCUSSION

To guide future study of the dynamics of dominance, we have proposed the concept of a longitudinal hierarchy: the characterization of a single, latent hierarchy and it's dynamics over time (**Figure 2.1**). In the longitudinal hierarchy framework, rank orders (*r*) and hierarchy dynamics (Δ) are inferred as a function of a period delineation rule (*p*), the interaction data, and ranking method. Hierarchy dynamics are calculated as changes in an individual's rank from one study period to the next, and can result from active processes (Δa) or passive processes (Δp). Studies inferring longitudinal hierarchies should thus clearly describe the type of dynamics under consideration (Δ , Δa , or Δp) and the *p*, the interaction data, and the ranking method used to infer the hierarchy.

Although rank dynamics are often extremely important to the biology of social animals, a lack of guidelines on how to reliably estimate Δ has until now limited our ability to study them. To facilitate studies of hierarchy dynamics we developed improved versions of three existing ranking approaches, and provide these and other tools for longitudinal hierarchy inference in a new R package, called DynaRankR. We evaluated these three methods and their original counterparts with respect to their ability to accurately infer rank dynamics and rank orders.

Results from empirical and simulated datasets reveal that method choices have profound effects on the inferred longitudinal hierarchies, most notably on Δ . Our primary finding is that methods that update ranks from previous periods and incorporate prior knowledge of dominance correlates infer longitudinal hierarchies with more accurate Δa

than methods that do not take advantage of existing information. In contrast, the choice of method did not significantly affect estimates of Δp in any of our analyses. This result is unsurprising, as Δp is primarily driven by numbers of individuals joining and leaving the social group, which is invariant across methods. Thus, our results show that method choices influence estimates of overall hierarchy dynamics via their variable estimates of Δa . The greater efficacy of the informed methods over their uninformed counterparts suggests that updating ranks from previous periods is vital to the accurate estimation of longitudinal hierarchies. We therefore conclude that inference of longitudinal hierarchies is inappropriate when using methods that infer ranks *de novo* in each study period.

Our results also suggests that incorporation of prior knowledge of dominance correlates improves the ability to estimate accurate longitudinal hierarchies. Obviously, this strategy is dependent upon a previously identified dominance correlate or acquisition rule (e.g., maternal rank inheritance with youngest ascendancy), and some organisms may not yet be sufficiently well-studied to identify such a pattern, or no such pattern may exist at all. However, we foresee the incorporation of prior knowledge of dominance correlates to be useful for a wide variety of organisms; hierarchies based on status badges (e.g., Tibbetts & Dale 2004), tenure- or inheritance-based rank acquisition (Lea, Learn, Theus, Altmann, & Alberts, 2014), or hierarchies based on size, age or weapon size [64,65] may all provide the basis for such an approach.

Although not the focus of our study, the choice of period delineation rule (p) is another methodological decision that can potentially influence inference of longitudinal hierarchies. As a preliminary investigation into the effect of p, we divided the female hyena dataset based on larger and smaller values of p in addition to our original

analysis using year-long periods. **Figure 2.8** depicts estimates of Δa inferred by each of the informed methods when periods were divided daily, yearly, and every two years. Period length did have an effect on estimates of Δa , with daily periods leading to more inferred dynamics in female hyena hierarchies than the other two choices of *p*.



Figure 2.8. Hierarchy dynamics identified by each informed method in the empirical dataset from female spotted hyenas as a function of period length. Periods were created based on observations conducted daily, yearly, or every two years. Each boxplot depicts the distribution of the number of positions each individual moved due to active processes over the course of its time in the study.

Because our simulation studies suggest that all methods are likely to overestimate hierarchy dynamics when the underlying hierarchy is stable, it is likely that inferring this longitudinal hierarchy with daily periods is inappropriate. However, more research is needed to investigate the optimal choice of p, and previous work provides conflicting guidelines. Neumann et al. (2011) argue for short p, such as one interaction per period, because this way demographic and rank changes can't occur mid-period. However, work by Flack and colleagues [66–68] has shown that information encoded at larger time-scales is more predictive of the future state of conflict networks than the fine-scale

outcomes of individual interactions, and that individuals actually encode and use information over large time-scales to inform their behavior. This body of work suggests that inference of longitudinal hierarchies with short periods may overestimate hierarchy dynamics, which is consistent with our finding in hyenas that daily periods result in more inferred dynamics than do periods of one or two years. Overall, we hesitate to provide overly specific guidelines on selection of p, and instead advise consideration of the biology of the organism when selecting p (i.e., what is a meaningful time-scale for this organism?), and caution against comparing longitudinal hierarchies that are inferred using different p rules.

In light of our results, which method should one use to infer longitudinal hierarchies? In all empirical and simulated datasets, Informed MatReorder produced the most conservative values of Δa of the three methods, Informed David's Scores produced intermediate values of Δa , and Informed Elo inferred the most dynamics of the three methods (**Figures 2.3, 2.4, 2.7, 2.8**). These differences led Informed MatReorder to perform best when the true latent hierarchy was most stable, and the Informed David's Score to perform best when the true latent hierarchy was more dynamic. Prior reports on the study organism can therefore be used to select a method that corresponds to what has been reported about that species. For example, most vertebrate hierarchies are stable most of the time, although periods of extreme instability can arise as a result of deaths of key individuals or new individuals entering the group [69]. In the case of spotted hyenas and other matrilineal species, prior reports suggest that ranks relationships change very infrequently, so Informed MatReorder is the most appropriate choice. However, the choice of ranking method may also depend

upon the goals of the study. Informed MatReorder is only sensitive to full reversals of prior dominance relationships, whereas Informed Elo and Informed David's Score are sensitive at the level of individual interactions. Therefore, researchers who are interested in studying lasting changes in rank relationships should use Informed MatReorder, whereas those interested in uncertain dominance relationships or fine-scale fluctuations should opt for Informed Elo or Informed David's Score.

Despite its challenges, the estimation of longitudinal dominance hierarchies allows for greater understanding of the forces that have led to the evolution of unequal societies across taxa, and is thus worthy of further study. Long-term data provide the opportunity to detect patterns that operate on a scale larger than would be detectable by short-term studies [70], and thus reliable methods for extracting dominance information from longitudinal data will enable new perspectives on dominance. The framework and methods advanced here will facilitate study of the causes of hierarchy dynamics and the relative contribution of active and passive processes to these dynamics. Future directions to expand upon this work include development of techniques for measuring Δa and Δp with numerical dominance scores, further investigating the effects of choice of the period delineation rule, and consideration of the influences of hierarchy steepness. Our future applications of this framework will investigate the dynamic structure of social inequality, and the role of individual traits, socioecological factors, and social bonds in shaping animal societies.

APPENDICES

APPENDIX A: Informed MatReorder method description

This section explains the reordering algorithm implemented in the Informed MatReorder ranking method. This method is implemented by the *informed_matreorder* function in the DynaRankR package [43].

Update initial order

Informed MatReorder selects an optimal order for each period by modifying the order from the previous period to minimize the proportion of dyadic relationships inconsistent with the data while retaining as much of the structure from the previous period as possible. The algorithm starts by creating an initial order for the current period based on the order from the previous period. In the special case of the first period, where no previous period exists, the order supplied by the user as the 'initial ranks' argument is treated as the previous order. Dead or emigrated individuals are then removed from the order and new individuals are added to the hierarchy according to the dominance correlate (in the *informed_matreorder* function this is specified by the user using the 'convention' argument, and dominance correlate data appear in the 'contestants' argument).

Create sociomatrix and (optionally) validate inconsistencies

Next, the algorithm adjusts this initial order by tabulating all outcomes of observed agonistic interactions in a sociomatrix, and binarizing the matrix such that a 1 appears in cells where the row individual beat the column individual more than vice

versa, and a 0 appears in cells where the row individual lost to the column individual more than vice versa. Cells for dyads that don't interact or where both individuals win equal numbers of interactions also receive 0s. Inconsistencies are identified as dyads with an observed winner that is not consistent with the proposed order. If require.corroboration = TRUE, inconsistencies are removed from the matrix if there are no subsequent observations of the dyad that corroborate the inconsistency.

Reordering process

The order is then optimized in a multi-step reordering process similar to that implemented in the I&SI method [1,47]. The optimization criteria are (first) to minimize the number of inconsistencies, and (second) to minimize the difference between the proposed order and the previous order. This process takes place iteratively according to the specified number of reordering attempts (n), in which multiple shuffling steps (shuffles) are taken. For each shuffle step, every individual involved in an inconsistency is attempted to be moved, and the order in which they are moved is chosen randomly. Each individual is tried in every potential new location; each time an order is identified with fewer inconsistencies than the previous best order, it is saved as the new best order. If an order is produced that has an equal number of inconsistencies with the best order, it is saved in addition to the previous best order, such that 'best order' is a list of orders with the same number of inconsistencies. If there are multiple 'best orders' when an individual is being selected to be moved, the order to be modified is randomly selected from the subset of 'best orders' that are most similar to the previous order. Once all individuals who were involved in an inconsistency have been considered in

new locations, the shuffling step is over. This process is repeated until no new orders are identified in a shuffling step or the user-specified number of shuffling steps have all been completed. All orders in the 'best orders' list are then saved to a 'master list'. This process is repeated by the number of specified reordering attempts (n), and the 'master list' accumulates all orders in the 'best orders' list from each reordering attempt. The 'master list' is then filtered to remove any orders that have more inconsistencies than the others.

Selection of final order

Finally, the optimal order is selected from the 'master list' by comparing the similarity between order in the list and the initial order from the current study period (i.e., the order from previous period with demographic changes incorporated). Similarity is assessed as the proportion of dyadic dominance relationships implied by each order where the orders agree on which dyad-member is dominant. For example, if one order lists A above B and the other lists B above A, the orders don't agree on the dominance relationship in this dyad. This measure of similarity is proportional to Kendall's correlation coefficient. Ties between equally optimal orders are broken by selecting the order that best fits, first, the observations from the current study period, then observations from subsequent study periods. If ties remain after these selection criteria are applied, a final order is selected randomly from among the tied orders.



APPENDIX B: Simulation results with less informative dominance correlate

Figure 2.B.1. Assessment of ranking methods using a mildly dynamic simulated latent hierarchy and <u>dominance correlate with a correlation to true order of 0.7</u>. Hierarchies were assessed under conditions of low (20%) medium (50%) and high (80%) proportions of missing data. a) Accuracy of methods, assessed as the proportion of dyadic relationships correctly identified during each period and b) parameter estimates for the effects of each method, with Informed MatReorder as the reference level (dashed line). c) Total magnitude of position changes due to active processes each individual underwent in the hierarchy inferred by the different methods and in the real simulated hierarchy. d) parameter estimates for the amount of change identified compared to the amount of change in the true hierarchy (dashed line). e) Example of one of the 10 simulated hierarchies used in this analysis. Note that confidence intervals are narrow for parameter estimates because of the large sample size.



Figure 2.B.2. Assessment of ranking methods using a mildly dynamic simulated latent hierarchy and <u>dominance correlate with a correlation to true order of 0.5</u>. Hierarchies were assessed under conditions of low (20%) medium (50%) and high (80%) proportions of missing data. a) Accuracy of methods, assessed as the proportion of dyadic relationships correctly identified during each period and b) parameter estimates and confidence intervals for the effects of each method, with Informed MatReorder as the reference level (dashed line). c) Total magnitude of position changes due to active processes each individual underwent in the hierarchy inferred by the different methods and in the real simulated hierarchy. d) parameter estimates and confidence intervals for the amount of change identified compared to the amount of change in the true hierarchy (dashed line). e) Example of one of the 10 simulated hierarchies used in this analysis. Note that confidence intervals are narrow for parameter estimates because of the large sample size.



Figure 2.B.3. Assessment of ranking methods using a mildly dynamic simulated latent hierarchy and <u>dominance correlate with a correlation to true order of 0.2</u>. Hierarchies were assessed under conditions of low (20%) medium (50%) and high (80%) proportions of missing data. a) Accuracy of methods, assessed as the proportion of dyadic relationships correctly identified during each period and b) parameter estimates and confidence intervals for the effects of each method, with Informed MatReorder as the reference level (dashed line). c) Total magnitude of position changes due to active processes each individual underwent in the hierarchy inferred by the different methods and in the real simulated hierarchy. d) parameter estimates and confidence intervals for the amount of change identified compared to the amount of change in the true hierarchy (dashed line). e) Example of one of the 10 simulated hierarchies used in this analysis. Note that confidence intervals are narrow for parameter estimates because of the large sample size.

APPENDIX C: Analysis of the immigrant male hierarchy

We tested the performance of the six ranking methods on 27-years of interaction data from immigrant male spotted hyenas belonging to the same social group as that used in the female analysis described in the main text. Unlike the maternal rank inheritance system in female spotted hyenas, immigrant male spotted hyenas queue for dominance, such that males with the longest tenure in the group occupy the highest rank positions [54,71]. We used this principal of tenure to add new males to the hierarchies in the three informed methods. New males were considered to have immigrated into the clan once they had been observed interacting with members of the clan on at least three different occasions. There were on average 20.59 (11-28) adult males, and there were on average 4.04 (0-9) individuals recruited and 4.04 (0-13) individuals lost from the group per year. Data from males were significantly more sparse than those from females, with an average of 4.36 interactions per male per year and a mean *% unknowns* per year of 82.29 (65.23-98).

Overall, the results from this analysis support our findings from the analysis of data from adult females, and demonstrate how the informed methods can be used with conventions of different types (i.e., maternal rank inheritance (females), tenure (males), physical attribute (simulations)).



Figure 2.C.1. (a-f) Visual depiction of the dominance hierarchies identified by each method from the 27-year empirical dataset from a wild population of immigrant male spotted hyenas. Each line represents the rank assigned to a single adult male over the course of his lifetime. Crossing lines indicate an identified reversal of a previously held dominance relationship (i.e., Δa), whereas non-crossing lines indicate stability from year to year in the identified longitudinal hierarchy. Numbers of rank positions varied with number of immigrant males present in the clan over time.



Figure 2.C.2. Hierarchy dynamics identified by each method in the empirical dataset from male spotted hyenas. Each boxplot depicts the distribution of the number of positions each individual moved due to active processes over the course of its presence in the study clan.

Comparison	Significance	Estimate	CI
I&SI - Informed MatReorder	***	2.06	[1.85, 2.27]
Informed Elo - Informed MatReorder	***	1.03	[0.8, 1.26]
Elo - Informed MatReorder	***	1.56	[1.34, 1.77]
Informed David's Score - Informed MatReorder	***	0.5	[0.25, 0.75]
David's Score - Informed MatReorder	***	2.02	[1.81, 2.23]
Informed Elo - I&SI	***	-1.03	[-1.16, -0.89]
Elo - I&SI	***	-0.5	[-0.62, -0.39]
Informed David's Score - I&SI	***	-1.56	[-1.73, -1.39]
David's Score - I&SI		-0.04	[-0.14, 0.06]
Elo - Informed Elo	***	0.53	[0.38, 0.68]
Informed David's Score - Informed Elo	***	-0.53	[-0.72, -0.33]
David's Score - Informed Elo	***	0.99	[0.85, 1.13]
Informed David's Score - Elo	***	-1.06	[-1.23, -0.88]
David's Score - Elo	***	0.46	[0.35, 0.58]
David's Score - Informed David's Score	***	1.52	[1.35, 1.69]

Table 2.C.1. Pairwise comparisons of hierarchy dynamics identified by each method in the empiricaldataset from male spotted hyenas. Compare to Figure 2.C.2



Figure 2.C.3. The proportion of observed outcomes of agonistic interactions between immigrant adult male spotted hyenas and the rank orders identified by each method. Data from (a) were from a current year in the study and were used to produce the order. Data in (b) were from the following study year. Disparities between the fit in (a) and (b) indicate overfitting. Letters indicate significantly different groups.

Comparison	Significance	Estimate	CI
I&SI - Informed MatReorder	***	0.94	[0.54, 1.33]
Informed Elo - Informed MatReorder		0.33	[0, 0.66]
Elo - Informed MatReorder		0.12	[-0.19, 0.44]
Informed David's Score - Informed MatReorder	***	-0.84	[-1.11, -0.57]
David's Score - Informed MatReorder		-0.08	[-0.38, 0.22]
Informed Elo - I&SI	***	-0.61	[-1.02, -0.2]
Elo - I&SI	***	-0.82	[-1.22, -0.42]
Informed David's Score - I&SI	***	-1.78	[-2.14, -1.41]
David's Score - I&SI	***	-1.02	[-1.41, -0.63]
Elo - Informed Elo		-0.2	[-0.54, 0.13]
Informed David's Score - Informed Elo	***	-1.16	[-1.46, -0.87]
David's Score - Informed Elo	**	-0.41	[-0.73, -0.08]
Informed David's Score - Elo	***	-0.96	[-1.24, -0.68]
David's Score - Elo		-0.2	[-0.51, 0.11]
David's Score - Informed David's Score	***	0.76	[0.5, 1.02]

Table 2.C.2 Pairwise comparisons of the proportion of observed outcomes of agonistic interactions in thecurrent year that are consistent with the order generated for that year. Data from adult male spottedhyenas. Compare to Figure 2.C.3a

Comparison	Significance	Estimate	CI
I&SI - Informed MatReorder		-0.23	[-0.48, 0.02]
Informed Elo - Informed MatReorder		-0.13	[-0.38, 0.13]
Elo - Informed MatReorder	***	-0.41	[-0.66, -0.17]
Informed David's Score - Informed MatReorder	***	-0.55	[-0.8, -0.31]
David's Score - Informed MatReorder	***	-0.5	[-0.74, -0.25]
Informed Elo - I&SI		0.1	[-0.14, 0.35]
Elo - I&SI		-0.18	[-0.42, 0.05]
Informed David's Score - I&SI	***	-0.32	[-0.55, -0.09]
David's Score - I&SI	*	-0.27	[-0.5, -0.03]
Elo - Informed Elo	**	-0.29	[-0.53, -0.05]
Informed David's Score - Informed Elo	***	-0.43	[-0.66, -0.19]
David's Score - Informed Elo	***	-0.37	[-0.61, -0.13]
Informed David's Score - Elo		-0.14	[-0.36, 0.09]
David's Score - Elo		-0.08	[-0.31, 0.14]
David's Score - Informed David's Score		0.06	[-0.16, 0.28]

Table 2.C.3 Pairwise comparisons of the proportion of observed outcomes of agonistic interactions inthe subsequent year that are consistent with the order generated for the current year. Data from adultmale spotted hyenas. Compare to Figure 2.C.3b

APPENDIX D: Pairwise comparisons for analysis of female hyena data

Comparison	Significance	Estimate	CI
I&SI - Informed MatReorder	***	3.43	[3.11, 3.75]
Informed Elo - Informed MatReorder	***	1.97	[1.63, 2.31]
Elo - Informed MatReorder	***	2.72	[2.39, 3.04]
Informed David's Score - Informed MatReorder	***	1.6	[1.26, 1.95]
David's Score - Informed MatReorder	***	3.39	[3.07, 3.71]
Informed Elo - I&SI	***	-1.46	[-1.59, -1.33]
Elo - I&SI	***	-0.71	[-0.81, -0.61]
Informed David's Score - I&SI	***	-1.82	[-1.98, -1.67]
David's Score - I&SI		-0.04	[-0.12, 0.04]
Elo - Informed Elo	***	0.74	[0.6, 0.89]
Informed David's Score - Informed Elo	***	-0.37	[-0.55, -0.18]
David's Score - Informed Elo	***	1.42	[1.29, 1.55]
Informed David's Score - Elo	***	-1.11	[-1.28, -0.95]
David's Score - Elo	***	0.67	[0.57, 0.77]
David's Score - Informed David's Score	***	1.79	[1.63, 1.94]

Table 2.D.1. Pairwise comparisons of hierarchy dynamics identified by each method in the empiricaldataset from female spotted hyenas. Compare to **Figure 2.6** in main text.

Comparison	Significance	Estimate	CI
I&SI - Informed MatReorder	***	-0.34	[-0.51, -0.17]
Informed Elo - Informed MatReorder		0.14	[-0.04, 0.33]
Elo - Informed MatReorder		-0.17	[-0.34, 0]
Informed David's Score - Informed MatReorder	***	-0.24	[-0.41, -0.07]
David's Score - Informed MatReorder	***	-0.55	[-0.71, -0.38]
Informed Elo - I&SI	***	0.48	[0.31, 0.66]
Elo - I&SI	*	0.17	[0.01, 0.33]
Informed David's Score - I&SI		0.1	[-0.06, 0.26]
David's Score - I&SI	**	-0.2	[-0.35, -0.06]
Elo - Informed Elo	***	-0.31	[-0.49, -0.13]
Informed David's Score - Informed Elo	***	-0.38	[-0.56, -0.21]
David's Score - Informed Elo	***	-0.69	[-0.86, -0.52]
Informed David's Score - Elo		-0.07	[-0.24, 0.09]
David's Score - Elo	***	-0.38	[-0.53, -0.22]
David's Score - Informed David's Score	***	-0.3	[-0.46, -0.15]

Table 2.D.2 Pairwise comparisons of the proportion of observed outcomes of agonistic interactions inthe current year that are consistent with the order generated for that year. Data from female spottedhyenas. Compare to Figure 2.7a in main text.

Comparison	Significance	Estimate	CI
I&SI - Informed MatReorder	***	-0.91	[-1.1, -0.72]
Informed Elo - Informed MatReorder	***	-0.38	[-0.59, -0.17]
Elo - Informed MatReorder	***	-0.82	[-1.01, -0.62]
Informed David's Score - Informed MatReorder	***	-0.38	[-0.58, -0.17]
David's Score - Informed MatReorder	***	-1.03	[-1.22, -0.84]
Informed Elo - I&SI	***	0.53	[0.36, 0.7]
Elo - I&SI		0.09	[-0.07, 0.25]
Informed David's Score - I&SI	***	0.53	[0.36, 0.71]
David's Score - I&SI		-0.12	[-0.27, 0.03]
Elo - Informed Elo	***	-0.44	[-0.61, -0.26]
Informed David's Score - Informed Elo		0	[-0.19, 0.19]
David's Score - Informed Elo	***	-0.65	[-0.82, -0.48]
Informed David's Score - Elo	***	0.44	[0.26, 0.62]
David's Score - Elo	**	-0.21	[-0.36, -0.05]
David's Score - Informed David's Score	***	-0.65	[-0.82, -0.48]

Table 2.D.3 Pairwise comparisons of the proportion of observed outcomes of agonistic interactions in the subsequent year that are consistent with the order generated for the current year. Data from female spotted hyenas. Compare to **Figure 2.7b** in main text.



APPENDIX E: Simulation results with Elo parameter K=200

Figure 2.E.1. Assessment of ranking methods using a <u>mildly dynamic</u> simulated latent hierarchy. **Elo-rating methods were run with K = 200**. The results and conclusions from these analyses do not differ from the same analysis run with K = 100 (**Figure 2.3** in main paper).



Figure 2.E.2. Assessment of ranking methods using a <u>highly dynamic</u> simulated latent hierarchy. **Elo-rating methods were run with K = 200**. The results and conclusions from these analyses do not differ from the same analysis run with K = 100 (**Figure 2.4** in main paper).



APPENDIX F: Plots of dynamics due to passive processes (Ap)

Figure 2.F.1 Choice of method and % *unknowns* have no effect on the inferred dynamics due to passive processes (Δp). We include plots from simulations with a) few changes in the true simulated hierarchy and a dominance correlate that is highly correlated with true ranks, b) many changes in the true simulated hierarchy and a dominance correlate that is highly correlated with true ranks, and c) few changes in the true simulated hierarchy and a dominance correlate that is dominance correlate that is weakly correlated with true ranks.





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CHAPTER THREE

SOCIAL ALLIANCES IMPROVE RANK AND FITNESS IN CONVENTION-BASED SOCIETIES

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ABSTRACT

Social hierarchies are widespread in human and animal societies, and an individual's position in its hierarchy affects both its access to resources and its fitness. Hierarchies are traditionally thought of in terms of variation in individual ability to win fights, but many are structured around arbitrary conventions like nepotistic inheritance rather than such traits as physical strength or weapon size. These convention-based societies are perplexing because position in the hierarchy appears to be gained irrespective of individual physical ability, yet social status strongly affects access to resources and fitness. It remains unclear why individuals abide by seemingly arbitrary conventions regarding social status when they stand to benefit by ignoring these conventions and competing for top positions or access to resources. Using data from wild spotted hyenas collected over 27 years and five generations, we show that individuals who repeatedly form coalitions with their top allies are likely to improve their position in the hierarchy, suggesting that social alliances facilitate revolutionary social change. Using lifetime reproductive success as a fitness measure, we go on to demonstrate that these status changes can have major fitness consequences. Finally,

we show that the consequences of these changes may become even more dramatic over multiple generations, as small differences in social rank become amplified over time. This work represents a first step in reconciling the advantages of high status with the appearance of 'arbitrary' conventions that structure inequality in animal and human societies.

INTRODUCTION

It has long intrigued those interested in social evolution why egalitarian societies are so rare in both humans and other animals, and why some societies appear to be so much more unequal than others. Since the identification of a pecking order in chickens in 1922 [1], we humans have recognized in non-human animals a reflection of the inequality that characterizes our own societies. In many societies, this inequality manifests as a dominance hierarchy, in which consistent asymmetries in the outcomes of contests between individuals produce a network of dominance relationships. This in turn allows for each member of the group to be classified by the degree of privilege it enjoys in its interactions with group-mates, as an individual's position in the hierarchy usually has profound effects on its priority of access to resources during intragroup competition. Although some individuals benefit at the expense of others in these systems, all group members benefit from the stability that dominance hierarchies provide [2]. Past research has revealed widespread variability among animal societies with respect to the degree of inequality, the determinants of social status, and the social mobility possible within each society [3]. Although the forces underpinning variation in
social inequality are not well understood, it is clear that dominance hierarchies structure many important aspects of the lives of gregarious animals.

Occupying a high rank position in a dominance hierarchy can be tremendously beneficial with respect to both priority of resource access and fitness consequences [4]. These advantages suggest that the means by which individuals secure and maintain high social status are important components of individual fitness. An obvious means for acquiring dominance status involves direct competition between individuals; indeed, the primary techniques for identifying social status use the outcomes of aggressive interactions as indicative of social dominance [5,6]. There are, however, other forces that structure dominance relationships while also obviating potentially dangerous fights. Although the determinants of social status vary among species, these forces can usually be classified as one of two main types, either individual attributes or conventions.

In attribute-based hierarchies, dominance rank depends on physical or behavioral qualities of individual group members. These attributes can be morphological traits affecting ability to win fights [7] (e.g., body size in elephant seals (*Mirounga angustirostris*) [8]), ability to produce a behavioral display (e.g., piping in oystercatchers (*Haematopus ostralegus*) [9]), or a morphological display such as status badges (e.g., face masks in paper wasps (*Polistes dominulus*) [10]). Attribute-based dominance hierarchies have been well studied, and fluctuation in these attributes are associated with corresponding fluctuations in dominance status [e.g., 11]. Furthermore, these traits usually covary with body condition and circulating levels of testosterone [e.g., 12], suggesting that they are honest indicators of the ability to win fights.

In convention-based hierarchies, dominance rank is acquired through a convention such as tenure in the group [13], age [14] or maternal rank 'inheritance' [15], and these conventions appear to operate irrespective of individual quality (e.g., [16]). Surprisingly little is known about fluctuations in dominance status in convention-based societies, and the functioning of convention-based hierarchies is thus perplexing. If high dominance rank is desirable and the convention determining rank is not tied to individual quality, what prevents high-quality individuals from ignoring the convention and asserting dominance through other means? If rank reversals occur in these groups, how do individuals improve in rank at the expense of others?

Perhaps the most common convention-based dominance hierarchies are the 'nepotistic hierarchies' found in many cercopithecine primates and spotted hyenas *(Crocuta crocuta)*, in which dominance rank acquisition follows a pattern strikingly like genetic inheritance. Rather than a true genetic process, however, dominance rank is acquired through a behavioral 'inheritance' process that involves learning, and follows two general rules: (1) juveniles acquire status immediately below that of their mothers in a pattern dubbed 'maternal rank inheritance,' and (2) juveniles outrank their older siblings in a pattern called 'youngest ascendency' [17]. This process is dependent upon coalitionary support from kin and sometimes also from non-kin, and the mother's presence and support during aggressive interactions play especially important roles in ensuring that her offspring acquire their ranks according to these rules [18]. The fact that kin play an important role in rank acquisition in these societies suggests that individuals may gain inclusive fitness benefits by promoting rank acquisition in their relatives.

Whereas the forces underlying rank acquisition in these societies have been well studied, surprisingly little is known about how adults in nepotistic hierarchies maintain or alter their social status. Rank reversals occur rarely in these species, which is perplexing given the lack of quality-based traits structuring their hierarchies. Most documentation of rank reversals in these hierarchies comes from isolated observations of captive or semi-natural populations, sometimes after demographic manipulation [19-26], or occasionally from observations of wild populations [27,28]. The only systematic naturalistic studies of rank changes in nepotistic hierarchies focus specifically on reversals between aging females and their adult female offspring, and suggest that older females allow their daughters to overtake them when the indirect fitness benefits accrued from their daughter's reproductive potential outweigh their own reproductive value [18,29]. Aside from these specific cases of reversals between daughters and their aging mothers, no study to date has tested hypotheses suggesting forces that produce rank reversals among adults in wild nepotistic hierarchies. A common observation among studies documenting rank reversals, however, is coalitionary support during aggression among group members. Coalitionary aggression has also been implicated in rank reversals in hierarchies based on physical attributes in a variety of species [3], suggesting that polyadic aggression may also allow for cryptic competition over rank in convention-based societies. Across species, coalitions directed up the hierarchy, called 'revolutionary coalitions,' are considered a means by which lower ranking individuals can effect rank reversals (reviewed in [30]), and consequently may be important in driving rank reversals in nepotistic societies. In spotted hyenas, recent evidence points to social support as a driver of female dominance [31]. Overall, these studies implicate

coalitionary support as a mechanism underlying rank and rank reversals in conventionbased societies.

Here we use a longitudinal dataset from four wild groups of spotted hyenas to study the relationship between coalitionary bonds and rank reversals among adults in nepotistic hierarchies. Spotted hyenas are highly gregarious carnivores living in large, mixed sex groups called clans, each of which is structured by a strict matrilineal nepotistic dominance hierarchy in which rank strongly affects reproductive success [32]. Rank acquisition in hyenas rigidly follows the two rules of nepotistic rank inheritance [33], making these animals excellent models for the study of nepotistic hierarchies in general. Following from these observations, our study investigates whether coalitionary alliances with group-mates allow individuals in nepotistic hierarchies to improve their status. Specifically, we test the hypothesis that individuals who have strong coalitionary bonds are more likely to support one another in challenging higher-ranked individuals, and consequently are more likely to improve their status. This hypothesis predicts that (1) up-hierarchy coalitions will occur during rank reversals, (2) these coalitions will be more likely to occur between individuals who are more strongly bonded, and as a result, (3) individuals who engage in more coalitions with their top partners will be more likely than others to improve their social status. Finally, we also consider the long-term impacts of these rank reversals in terms of expected change in fitness during the lives of individual hyenas, and examine the intergenerational consequences arising from maternal rank inheritance.

RESULTS

Identification of rank reversals

We used the longitudinal hierarchy framework we advanced in a previous paper [34] to study rank reversals. In this approach, interaction data are divided into study periods spanning the length of the study, ranks are determined for each individual present in each period, and hierarchy dynamics are inferred as the difference in rank each individual occupies from one period to the next. Changes in an individual's rank can arise from passive processes, which include demographic changes (e.g., births, immigration). Active processes produce the remainder of rank dynamics; these changes, which we call here 'rank reversals,' arise when the members of a dyad reverse a previously held dominance relationship. For example, if an individual surpasses two of its group-mates, that individual will have undergone two rank reversals (because it reversed rank relationships with two individuals) and each surpassed individual will have undergone one rank reversal. Their rank change due to rank reversals associated with this event would be 2, -1, and -1, respectively. In our previous work, we found that ranking algorithms tend to overestimate the amount of active dynamics in a longitudinal hierarchy, and this shortcoming was particularly evident when used to infer simulated hierarchies with few true rank reversals.

Because spotted hyenas are reported to have highly stable hierarchies [31], we elected to use the Informed MatReorder ranking method, which we found to produce the most conservative estimates of rank reversals and to outperform other methods (Elorating [6], David's Score [28], I&SI [5]) in tests on stable simulated and empirical

hierarchies, including one of the hierarchies we investigate here [34]. Conservative estimates of rank reversals are particularly desirable in this study because too many false positives (i.e., identification of rank reversals when there truly were none) can easily obscure an existing pattern in the true, rarely occurring cases. In prior tests of Informed MatReorder and other methods on highly stable simulated societies, all methods overestimated the amount of change in the hierarchy, but Informed MatReorder was considerably closer to estimating true hierarchy dynamics than any other method [34].

Informed MatReorder is a matrix-reordering method derived from the widely used I&SI algorithm [5]. In both procedures, observations of agonistic interactions are tabulated in a sociometric matrix, which is then iteratively reordered to minimize inconsistences, or dyads in which the assigned rank positions of the two individuals are inconsistent with the outcomes of their interactions. I&SI is designed for inferring static hierarchies, and attempts to reorder all individuals to minimize the number and strength of inconsistencies. Informed MatReorder adapts I&SI to be used for inferring longitudinal hierarchies by adding two features: (1) it uses prior knowledge of dominance correlates characteristic of the study organism to inform placement of newly recruited individuals, and (2) ranks from a given period are determined by the ranks from the previous period, updated with new information. Importantly, this 'inertial tendency' for ranks to remain constant in the absence of data suggesting a change is essential to prevent overestimation of the number of rank reversals [34]. Thus, Informed MatReorder minimizes both the number of inconsistencies and the number of difference between the proposed order and the order from the previous study period. In

accordance with conventions of both maternal rank 'inheritance' and youngest ascendency, when a new individual is recruited into the group, Informed MatReorder adds her to the hierarchy below her mother and above her older sisters before performing the reordering step. Because maternal rank inheritance is such a predictable pattern in this species [33], cases where the reordering step moves new individuals upward or downward from this position are interpreted as rank reversals. More details on Informed MatReorder can be found in our previous paper [34]; functions for implementing the method are available through the DynaRankR R package [35].

We applied Informed MatReorder to agonistic interaction data from females in four free-ranging clans of spotted hyenas in the Maasai Mara National Reserve, Kenya. We assigned ranks to each female every calendar year; this admittedly arbitrary choice of period length was selected because spotted hyenas are long lived, non-seasonal breeders, because their interbirth intervals are seldom shorter than one year, and because we deemed one year a sufficiently long sampling period in which to summarize agonistic behavior at the individual and dyadic levels. To infer the longitudinal hierarchy, we used 12,505 aggressive interactions (mean = 11.53 interactions/individual/year, sd = 6.05, range = 1.44 -27.21) among 249 adult females; of these, 2,966 (23.72%) interactions involved coalitionary support. These interactions include only those in which there was a clear loser, indicated by stereotyped submissive behavior [36].

In our study population, most individuals (78.1%) acquired their rank according to the previously described patterns of maternal rank inheritance and youngest ascendancy, and rank relationships were predominantly stable over time (**Figure 3.1**),

with only 13.7% of rank assignments involving a rank reversal. However, we observed a total of 141 cases of individuals changing rank due to rank reversals over the course of our study, with 43.1% of females changing rank due to rank reversal at some point in the study (which spanned the lifetime of many of the hyenas). Rank reversals did not primarily involve females overtaking their mothers; in 62 cases where females with known living mothers moved up the hierarchy, only 7 (11.3%) involved a daughter overtaking her mother.



Figure 3.1. Yearly ranks of each individual in each of four study clans. Crossing lines indicate rank reversals. By convention, lower numbers indicate higher ranks.

The role of coalitionary alliances in rank reversals

To measure the relationship between coalitionary support and rank change in the nepotistic hierarchies of spotted hyenas, we constructed yearly weighted non-directional networks of coalitionary interactions for each study clan. In these networks, the strength of ties between two individuals corresponds to the number of times those individuals

were observed engaging in concurrent aggression against a group-mate (n = 1913) coalitions with allied adult females); we identified each female's top allies as her three most frequent adult female coalition partners. To examine whether revolutionary coalitions were associated with rank reversals, we focused on 533 triadic coalitions where the two allied attackers and their target animal were all adult females. There were 33 triadic up-hierarchy coalitions, in which the target animal outranked both aggressors, and 464 triadic down-hierarchy coalitions, in which both allies outranked their target. We found that up-hierarchy coalitions occurred primarily in the context of rank reversals; 66.67% of up-hierarchy coalitions occurred during the year before or the year in which one or both aggressors surpassed the targeted individual through rank reversals. In contrast, only 0.43% of down-hierarchy coalitions occurred in the year in which or the year before the recipient surpassed one or both aggressors (χ^2 = 279.87, df = 1, p < 0.0001). Logistic mixed models with random effects of clan revealed that the probability of any coalition being directed up the hierarchy increased with the strength of the coalitionary bonds between the two aggressors, and this effect was significantly more extreme than in null models generated using permutation (ß = 0.187, standard error = 0.038, p = 0.033.; Figure 3.2).



Figure 3.2. The strength of bonds between coalition members predicts the probability that the coalition is directed up the hierarchy (often called 'revolutionary' coalitions). Histograms indicate the frequency of bond strengths for revolutionary (top) and down-hierarchy (bottom) coalitions, and bars in each category sum to 1. Rug plot lines below the histograms indicate the observed data.

Because of the non-independence of dyadic data such as those documenting coalitionary bonds, we assessed the significance of our models by comparing the observed effect of coalition bond strength to effects from null models where we ran the same regression on the data after conducting node-level permutation [37,38]. In this approach, the reported p-values denote the proportion of null models in which the effect of coalitionary bond strength was as extreme or more extreme than the effect estimated from the observed data. To further ensure that our observed effect of dyadic bond strength was not simply a function of the overall amount of coalitionary behavior in which each individual engaged, we made a similar model that included as a predictor

the total number of coalitions in which two allies engaged with all other adult females. This model was worse than the model using the strength of the dyadic bond as the predictor (Δ AICc = 9.27), and it was not significantly better than null models generated using permutation (β = 0.029, standard error = 0.007, p = 0.278). We also found that uphierarchy coalitions were significantly more likely to occur between top allies than other allies (χ^2 = 10.13; df = 1; p = 0.0015). These results suggest that, as individuals engage in more coalitions together, they become more willing to support one another in challenging dominant individuals. We lacked complete pedigree data for some subjects in this study, so we were unable to evaluate the role of kinship. However, prior work has found that spotted hyena females prefer to form coalitions with their kin [31,39], so kinship is a likely mediator of the formation of these strong coalitionary bonds.

To examine the overall effect of social allies on rank reversals, we constructed a linear mixed model modeling the yearly number of positions each individual moved upward or downward in the adult hierarchy due to rank reversals as a function of the strength of coalitionary bonds with its top three preferred coalitionary partners in that year. Because rank reversals are non-independent observations, we again used node-level permutation to compare the observed effect of coalitionary tie strength against the distribution of effects from null-models that preserve this non-independent structure, and calculated p-values as the proportion of null models with coefficient estimates as extreme or more extreme than our observed estimates. We found that coalitionary tie strength was strongly positively associated with the direction and magnitude of rank change, that this effect was more extreme than expected from null models generated using permutation ($\beta_{coalition ties} = 8.16$, standard error = 1.27, p = 0.001; $\beta_{coalition ties squared} =$

9.72, standard error = 1.19 p = 0.001; **Figure 3.3**), and that the model with coalitionary support as a predictor performed better than the model without it (Δ AICc = 118.2). This relationship was still significant after removing the two individuals with the most rank reversals ($\beta_{\text{coalition ties}}$ = 1.83, standard error = 1.01, p = 0.035; $\beta_{\text{coalition ties squared}}$ = 1.94, standard error = 0.92 p = 0.016), although examination of these data suggests no reason for their exclusion.



Figure 3.3. Individuals engaging in more coalitions with their top allies are more likely to increase their rank by surpassing their groupmates. Inset depicts model parameter estimates (open circles) from the linear mixed model and expected parameter estimates under the null hypothesis (black bars) derived from permuted networks. An offset for the number of observation sessions in which each individual was observed in each year was included in the model to account for varying numbers of observations among individuals.

Expected fitness consequences of rank reversals

To estimate the potential fitness consequences of the observed rank reversals, we modeled the relationship between mean rank and lifetime reproductive success (LRS) for females who we observed from birth until death. LRS for each female was calculated as the total number of offspring she produced that survived to reproductive maturity (2 years old). We restricted the analysis to 96 females who survived to at least four years old to eliminate individuals who died soon after puberty. Mean LRS for our study population was 2.28 (standard error = 0.27; range = 0 to 13), which is similar to the LRS of 2.36 ± 1.90 reported for a Tanzanian population of spotted hyenas [32]. We modeled an exponential relationship between mean lifetime rank and LRS using a Poisson generalized linear mixed model, and found that rank had a significant positive effect on LRS ($\beta_{rank} = 0.48$, standard error = 0.10, p < 0.0001; Figure 3.4a), which is consistent with earlier work [40]. Using this model, we estimated the expected changes in LRS due to the observed rank reversals (Figure 3.4b). We found that the expected fitness effects of rank reversals vary with the number of rank positions moved and where in the hierarchy they occurred. Most changes were single-position changes in the lower tiers of the hierarchy and had little effect on expected fitness (Figure 3.4c). However, expected fitness consequences were larger for rank reversals among highranked individuals and for rank reversals amounting to large position changes regardless of hierarchy position; here, some females experienced more than a two-fold change in their expected fitness.



Figure 3.4. Rank reversals are expected to have large fitness effects. (a) Data from 96 females for which we calculated lifetime reproductive success (LRS). Rank is a significant predictor of LRS. (b) The predicted fitness consequences of observed rank reversals, based on the model from (a). (c) Large expected fitness effects result from both rank changes occurring in the upper tier of the hierarchy and rank changes of large magnitude resulting from many simultaneous rank reversals. However, single rank reversals among low ranked individuals are predicted to have minimal fitness effects. Larger points indicate larger absolute values of predicted effects on fitness. Predicted fitness effects are colored according to the ratio of expected LRS in the new position relative to the expected LRS in the old position, with values <1 indicating a decline in LRS and values >1 indicating an increase in LRS.

We also examined the intergenerational effects of rank reversals. A mathematical

consequence of maternal rank inheritance and higher fitness among high-ranking

individuals is that individual rank declines over time as offspring born to higher-ranking

females join the adult hierarchy. As a result, small differences in rank between females

are expected to be amplified over time. Furthermore, this amplification is expected to continue over generations, such that descendants of two females of adjacent rank at time *t* could occupy rank positions separated by many individuals at future time points. Thus, a rank reversal producing a small change in rank between two hyenas at a single time point can later have large consequences for the ranks of their descendants. In this way, rank dynamics due to active processes can be amplified by rank dynamics due to passive processes.

To examine this effect more closely, we calculated the average difference in rank between the female descendants of heads of four matrilines that were adjacently ranked in the first year of our study in our longest-studied group (Figure 3.5a). We found that rank distance between the descendants of females from adjacently ranked matrilines increased considerably over time as a result of maternal rank inheritance and rankrelated reproductive success, and this difference was most dramatic between the alpha and beta matrilines (Figure 3.5b). As a result, descendants of females who were highranking in the first year of our study occupied very low rank positions decades later. This is consistent with the idea that the consequences of a rank reversal may become amplified over time. For example, from 2007-2009, a female from the "79" matriline surpassed four females from the "03" and "dj" matrilines (Figure 3.5a, female marked with diamonds). By 2014, the difference in rank between her current position and where she would have been in the absence of this change had increased to six, because the females that she had surpassed successfully reared offspring that would have otherwise outranked her. Not only was the magnitude of her rank change amplified, but, because her subsequent offspring inherited her new rank, her descendants also gained from this

rank reversal. Although we elected not to model the expected amplification of the observed rank reversals to avoid extrapolation from limited observations, there is a strong tendency for descendants of adjacently ranked females to occupy increasingly disparate ranks over long time scales, particularly among high ranking matrilines.



Figure 3.5. Rank differences among females in adjacent matrilines are amplified over time due to rank-related variation in reproduction and maternal rank inheritance. (a) The ranks of descendants from four original females in four matrilines occupying adjacent rank positions from 1988 through 2014. Only these four matrilines were considered because the others either died out or departed during clan fission events to form new clans (those females listed as 'other'). (b) The difference in rank between descendants of adjacent matrilines increases over time due to the addition of newly-reproductive females to the clan's dominance hierarchy. As a result, a rank change at any given time point may become amplified into large rank differences.

DISCUSSION

Here we provide the first systematic study of rank reversals among adult females in a convention-based nepotistic society. In these societies, rank is thought to be acquired through a convention of maternal rank inheritance rather than through displays or fighting, and rank reversals are uncommon. We find that, although rare, rank reversals do occur in convention-based hierarchies, are associated with coalitionary bond strength, and can have significant fitness consequences for the individuals involved. Our results showing that differences in matrilineal rank are amplified over multiple generations suggest that the long-term fitness consequences of rank reversals may be larger than we could measure directly. The combination of female philopatry, rank-related variation in reproductive success, and maternal rank inheritance results in a large decrease in an individual's rank over time as offspring of higher-ranking females enter the hierarchy above her. A female overtaking a group member in a rank reversal at any given time point might not only increase her LRS, but also increase the average rank and fitness of her future offspring. Although we were able to demonstrate that small rank differences between females were amplified over time (Figure 3.5b), we were not able to estimate the expected inclusive fitness benefits of these changes because of currently incomplete pedigree data. An important consideration when assessing inclusive fitness effects is the kinship structure of these societies. Because female relatives occupy adjacent positions within the dominance hierarchy, a female hyena engaging in rank reversal is likely to be related to the individuals she surpasses. Thus, females engaging in rank reversals are not only gaining inclusive fitness by

improving the rank of their descendants, but they are also incurring costs to their inclusive fitness by reducing the rank of more distant kin. Future studies with complete relatedness data should examine the inclusive fitness consequences of rank reversals in societies with maternal rank inheritance.

Although our models suggest that rank reversals can have important fitness benefits for individuals moving up the hierarchy, we have yet to quantify the immediate costs of attempting revolutionary coalitions. Engaging in up-hierarchy aggression, even with a coalitionary ally, has the potential to result in serious injury. In our study population, we have observed occasional extreme escalated aggression when lowerranked females challenge higher-ranked females, although our data are currently insufficient to assess the prevalence or the consequences of this extreme aggression. However, considerable evidence from hierarchies structured by direct competition suggests that rank challenges are associated with high risk of injury or death for the combatants [41]. Furthermore, there may be costs associated with rank reversals that do not result directly from escalated aggression over rank. Engaging in coalitionary aggression with social partners, even if only in low-level aggression directed down the hierarchy, is also likely to incur risk and energetic costs [30]. Finally, uncertainty about the state of the hierarchy produced by rank reversals is associated with increased stress for both the individuals directly involved and other group members, suggesting that challenges over rank may incur costs for the entire group [2,42]. It remains unclear to what extent these costs offset the potential benefits of rank reversals in conventionbased hierarchies.

Our results provide the first strong evidence of coalition-based competition resulting in rank changes in a convention-based hierarchy and are therefore consistent with recent challenges to the strict distinction between attribute-based hierarchies and convention-based hierarchies [18]. These results strongly support the conclusions of a recent study investigating the importance of social support in dominance in spotted hyenas [31]; evidently, in these societies, social support is a crucial component of social status and its dynamics. Coalitionary support in competition is neither an individual attribute nor a societal convention, but it may depend on both. Across convention- and attribute-based societies, individuals lending coalitionary support during aggressive interactions nearly always side with the dominant individual against the subordinate [39], which means that in convention-based hierarchies, the convention determining rank is a good predictor of patterns of coalitionary support. However, individual social aptitude may also be important in garnering coalitionary support. Thus, both individual attributes and convention can potentially play important roles in societies where coalitionary support is a force structuring rank. Future research should investigate the role of individual attributes in predicting rank reversals in convention-based hierarchies.

METHODS

Modeling up-hierarchy coalitions and rank changes

Spotted hyenas live in large, mixed-sex groups characterized by high degrees of fission-fusion dynamics, meaning that group members associate in subgroups that change composition frequently throughout the day. We modeled the relationship

between strength of coalitionary bonds and up-hierarchy aggressive attacks with a binomial GLMM. The dependent variable was the probability that a given coalition was directed up vs down the hierarchy, and the predictor was the strength of the coalitionary tie between members of the allied dyad in the year of the observed interaction. Bond strength was measured as the total number of polyadic agonistic interactions in which at least two adult females were allied against another. We initially included random effects for dyad, clan and year nested within clan because of repeated observations at each of those levels, but all except clan were dropped because they were estimated to explain 0 variance. To account for non-independence between observations of up- and downhierarchy coalitions, we conducted node-level permutations and ran the model with the permuted data. In these permutations, each coalition was assigned a random direction (i.e., up- or down-hierarchy) from the pool of coalitions observed in that clan in that year. Following suggested guidelines [37,38], we performed this permutation 1000 times and compared our observed effect to the distribution of effects from the permuted data to assess statistical significance.

We modeled the relationship between the yearly rank change each individual underwent and its alliance strength using a linear mixed model with random effects for individual identity, clan, and year nested within clan, although the latter two effects were dropped because they were estimated to explain 0 variance. We measured alliance strength as the sum of coalitionary ties with the three group-mates with strongest ties, akin to what has been done elsewhere [43]. We included the log of the total number of observation sessions involving that individual in that year as an offset in the model to account for differences in observation effort. We elected to control for observation at the

individual level rather than the dyadic level because we wanted to control for variability in observation of individuals rather than variability in their social relationships. In the fission-fusion societies of spotted hyenas, dyadic association rates reflect the animals' social preferences [31,39]. Observations of rank reversals are not independent of one another, so we again assessed statistical significance by permuting the observations of number of positions moved due to rank reversals among individuals within clan and year. We compared the observed effect of alliance strength on the amount and direction of rank change with the effects from 1000 models with permuted data. In the outlier analysis, the random effect of identity explained no variance and was causing convergence problems, so we repeated the same procedure as above but without the random effect.

Assessing fitness effects

Because of the rarity of rank reversals and the long lives of hyenas, we did not have the statistical power to directly measure the fitness consequences of the observed rank reversals. We estimated expected fitness effects using the lifetime reproductive success of 96 adult females for which we had complete lifetime reproductive data and who survived to at least four years of age. We modeled the total number of offspring they produced as a function of their mean rank over their lifetime. Rank was standardized to range from -1 (lowest in group) to 1 (highest in group). We modeled an exponential relationship between mean rank and lifetime reproductive success because model comparison with AIC revealed this model to be superior to models with linear relationship (Δ AIC = 4.08) or quadratic relationships (Δ AIC = 2.75).

To study the intergenerational consequences of rank reversals, we examined the relative change in ranks of descendants of four females from adjacent matrilines over time. We only considered matrilines in which descendants of original females in 1988 remained present in the group at the end of our study period. Descendants from all other matrilines had either died or had split off to form entire new clans. We did not include the other three study groups because we did not know the matrilineal kin relationships among most females at the start of the study. We also excluded individuals who changed rank in the calculation of these average rank differences because we were interested in understanding the expected change in rank in the absence of rank reversals.

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CHAPTER FOUR

FITNESS CORRELATES OF TRANSIENT EARLY-LIFE DEVIATION FROM EXPECTED RANK ACQUISITION PATTERNS

ABSTRACT

Social rank has been identified as a significant determinant of fitness in a variety of species. The importance of social rank suggests that the process by which juveniles come to establish their position in the social hierarchy is a critical component of social development. Here, we use the highly predictable process of rank acquisition in spotted hyenas to study the consequences of variation in rank acquisition in early life. In spotted hyenas, rank is 'inherited' through a behavioral learning process called 'maternal rank inheritance.' This pattern is highly predictable: ~80% of juveniles acquire the exact rank predicted by the rules of maternal rank inheritance. This predictable nature of rank acquisition in these societies allows the process of rank acquisition to be studied independently from the ultimate rank that each juvenile attains. In this study, we use a novel application of the Elo-rating method to calculate each juvenile's deviation from expected pattern of maternal rank inheritance during development. Despite variability in rank acquisition in juveniles, most of these juveniles come to attain the exact rank expected of them according to the rules of maternal rank inheritance. Nevertheless, we find that transient variation in rank acquisition in early life predicts long term fitness consequences for these individuals: juveniles 'underperforming' their expected rank show reduced survival and reduced lifetime reproductive success. Finally, we present evidence that this variability in rank acquisition in early life can be a source of early life

adversity, and that multiple sources of early life adversity have cumulative, but not compounding, effects on fitness.

INTRODUCTION

Social organisms experience costs and benefits from spatiotemporal overlap with their groupmates. Advantages of group living such as reduced predation risk, cooperative breeding, and cooperative resource defense, are weighed against costs such as increased competition over local resources, pathogen transmission, and risk of social conflict. In most societies, these costs and benefits are not experienced by all group members equally; some individuals gain more of the benefits and suffer fewer of the costs than others [1,2]. In animal societies, this disparity among group-mates emerges as a dominance hierarchy, where individuals differ systematically in their ability to defeat others in agonistic interactions [3]. A useful abstraction of the complex and unequal relationships among group members is 'rank,' which describes the extent to which an individual is able to exert power over its group-mates. Extensive research from a variety of organisms has demonstrated that individuals of high rank (in other words, are able to exert power over most other individuals in the social group) enjoy dramatic advantages as a result of their position in the social hierarchy, although species vary in the nature and strength of the relationship between social status and fitness [2,4–6].

In many species, the social status of adults are well predicted by certain phenotypes such as body size or physical markings, or certain conventions such as age or tenure [7–12]. Social factors, such as support from conspecifics or presence of kin,

also influence dominance rank [5,13–15]. Winner- and loser-effects, where individuals that win (lose) a particular interaction show increased probabilities of winning (losing) subsequent interactions, have also been demonstrated to affect hierarchy formation in a number of species [16,17]. Juvenile social rank appears to be influenced by these processes as well, although juveniles often aren't able to dominate adult group-mates until late in development [18,19]. As a result, juveniles continually re-negotiate dominance relationships with their group-mates as they mature [18,20]. In sum, many forces have been found to influence the acquisition of social status by juveniles, and investigations focusing on among-individual variation in the development of social status reveals that this process is complex and difficult to predict [15,21]. Individuals are likely to vary in the speed and accuracy with which they acquire social rank, but it is not clear what consequences this variation has or even how to measure such variation.

Here we take advantage of the spotted hyena (*Crocuta crocuta*) social system to conduct a large-scale prospective study on the consequences of variation in rank acquisition among juveniles. Spotted hyenas acquire their rank through a process known as maternal rank inheritance with youngest ascendency. In this system, juveniles come to acquire the rank directly below their mothers and above their older siblings, and this system is found in many Cercopithecine primates in addition to spotted hyenas. Prior work has found that rank acquisition by this process is highly predictable: most (78.1%) females acquired the exact rank predicted by maternal rank inheritance with youngest ascendency [13] and were able to consistently dominate lower-born adult females around 18 months old [19]. Here we leverage the highly predictable nature of rank acquisition in developing juvenile spotted hyenas to study the fitness

consequences of variation in this process. To measure variation in rank acquisition, we develop the 'Elo deviance' method, which measures deviation from a hypothesized rank for each juvenile. We apply this method at three stages across development to determine the relationship between variation in the process of rank acquisition and survival and lifetime reproductive success.

METHODS

We examined the relationship between juvenile rank acquisition and fitness in spotted hyenas from four study clans in the Maasai Mara National Reserve in south-west Kenya. Spotted hyenas live in large mixed-sex clans characterized by highly fluid fission-fusion dynamics [22], meaning that individuals from the same clan associate in subgroups that change composition several times per day. Here ranks were determined yearly for all adult females who were at least 1.5 years old at the start of the calendar year using the Informed MatReorder method [13,23,24]. Juveniles were assigned their mother's rank until they were old enough to have a rank assigned to them directly at 1.5 years of age.

Spotted hyena life-history

Developing juvenile spotted hyenas pass through three important life-history stages. First, juveniles are typically born in litters of 1-3 at a natal den, where they reside for the first 2-3 weeks of life. Births are rarely observed, so birthdates for cubs are estimated to within +/- 7 days based on the cubs' appearance when first observed

[25]. Second, after 2-3 weeks, mothers move their offspring to a communal den to reside with all other juveniles within the clan until they are around 8-12 months old. During this den-dependent stage, juveniles rarely stray more than a few hundred meters from the shelter of den holes, and they regularly enter the den while resting or when threatened. Rank relationships among juveniles emerge while cubs live at the communal den. At the start of the communal den period, maternal rank has little influence on rank relationships among juvenile peers, but juvenile ranks closely match the maternal hierarchy by the time cubs become den-independent [26]. Third, juveniles achieve den-independence at around 8-12 months of age; here we defined denindependence as the date on which a juvenile had been observed over 200m from the den on four consecutive occasions [27]. During the den-independent life-history stage, juveniles no longer reside at the den, but instead travel freely throughout the territory and associate in subgroups with related and unrelated group-mates. Weaning takes place during this den-independent period. After reaching reproductive maturity at 2 years old, males typically begin to disperse to new clans where they can be reproductively active, whereas females begin reproducing in their natal clans. Mortality here was determined to have occurred when an individual was found dead or when at least 6 months passed without it being observed. Data were right-censored for all individuals who were still alive on December 31st, 2017. Among males, we were unable to distinguish unobserved mortality from dispersal after 2 years of age, so male mortality data were right-censored at 2 years old.

Elo deviance method

We developed a novel 'Elo deviance' method to measure variation in rank acquisition by juveniles. This method is based on the widely used Elo-rating method, which calculates a numerical dominance score for each individual in a social group. The Elo-rating method updates the relative dominance scores of individuals within the group after each observed interaction [28,29]. Scores for the winner and loser of each interaction change based on a constant K scaled by the expected probability of the observed outcome, and this probability is calculated by comparing the scores of the two individuals prior to the interaction. Outcomes that are consistent with the relative scores of the winner and loser prior to the interaction lead to a small increase in the winner's score and a small decrease in the loser's score. In contrast, unexpected outcomes, where the winner had a lower score than the loser prior to the interaction, lead to large score changes. Thus, the Elo-rating method is highly sensitive to unexpected outcomes [28,29].

The Elo deviance method, introduced here, assesses deviation from an expected pattern of contest outcomes by calculating the difference between the observed Elorating for a focal individual and the Elo-rating that individual would have attained under some prior hypothesis. In this study, the prior hypothesis is that of maternal rank inheritance, where the ranks among juveniles should be isomorphic with the ranks among their mothers. Thus, we calculate a juvenile's Elo-deviance score by subtracting its observed Elo-rating from the Elo-rating it would have received had it won or lost every interaction as expected based on its mother's social rank.

To ensure that any differences between an individual's observed and expected Elo-rating is due to their behavior and not to the behavior of other group-members, Elo deviance scores are calculated for each individual independently. Thus, aggressive interactions are first restricted such that they involve only the focal individual, and interactions can be further restricted based on the study question (e.g., only interactions among members of the same sex, only interactions during a specific time period). Observed Elo-ratings are then calculated for the individuals involved in interactions; here, we use K = 20 and starting score value = 0 for the calculations of all Elo-ratings. Expected Elo-ratings are then calculated based on the expected winner and loser of each interaction according to the hypothesis under investigation. An Elo deviance trajectory is calculated for the focal individual by subtracting its observed Elo-rating from its expected Elo-rating, and the Elo deviance is determined as the difference between observed and expected Elo-rating after the final interaction. Individuals who win and lose interactions according to the hypothesis earn Elo deviances close to 0, whereas individuals who lose unexpectedly or win unexpectedly earn Elo deviances below or above 0, respectively.

Using age-binned Elo deviance to assess the average timing of rank acquisition

To measure the general pattern of rank acquisition in spotted hyenas, we calculated Elo deviances for each observed cub in each month of life using the cub's interactions with all group-mates and summarized Elo deviances according to month of age. Each individual had its' Elo deviance calculated independently for each month of age (i.e., an individual's score was 'reset' at each month of age). The behavior of

individuals of a particular age was summarized by taking the standard deviation of Elo deviances of all individuals at that age. At ages where many individuals had contest outcomes that were not predicted by maternal rank, individuals had highly variable Elo deviances and thus that month of age had a large standard deviation in Elo deviances. At ages where contest outcomes of most individuals followed maternal rank, the standard deviation of Elo deviances for individuals at that month of age was closer to zero. To ensure that behavior at a given month of age was not unduly influenced by a few individuals, months of age in which we had Elo deviances for fewer than 20 individuals were excluded from the analysis. We expected the standard deviation of Elo deviances to decline during the early juvenile period up until some transition point at which most juveniles had fully acquired their maternal rank; after this transition point, we expected the standard deviation of Elo deviances to remain relatively constant across later months of age. To determine the month of age at which this transition takes place, we used piece-wise linear regression; we modeled the standard deviation of Elo deviances at each month of age as a function of age, and estimated a single break point using the bootstrap restarting algorithm implemented in the segmented R package [30,31].

Using Elo deviance to measure individual variation in rank acquisition

To measure individual variation in rank acquisition, we assessed Elo deviance for each juvenile at three different life-history stages. Because juvenile's acquire their ranks relative to their peers before developing relationships with the rest of their group-mates [19,26], we assessed Elo deviance based on interactions with peers only. First, we
assessed the state of rank acquisition relative to peers at the end of the den-dependent period as the Elo deviance at den independence. This deviance at den independence was calculated from interactions among den-dependent juveniles only. Second, we assess the state of rank acquisition at reproductive maturity as the Elo deviance calculated from interactions among den-independent juveniles (less than 2 years old). Importantly, these scores are not influenced by any interactions prior to den-independence; in other words, scores are 'reset' between life-history stages. Finally, we assess the state of rank acquisition at the end of the first year of adulthood (3 years old) based on the interactions between these same individuals and all other adults. At each life-history stage, we calculated Elo deviances for only those individuals who survived to the end of the period over which we calculated Elo deviance for that life-history stage and only those individuals who were observed engaging in aggressive interactions during this period.

Modeling survival

We modeled survival as a function of Elo deviance at each of these three lifehistory stages using cox proportional hazards models. In addition to the Elo deviance specific to the life-history stage, we also included maternal rank (calculated as the rank the juvenile's mother held in the year of the juvenile's birth), and coded it categorically as 'high' and 'low' rank. To control for the possible influence of variable sampling on Elo deviance measures, we included the number of interactions used to calculate Elo deviance as a predictor in each model. Additionally, we included a binary predictor coding whether the juvenile's mother survived until the juvenile reached adulthood (2

years old). This predictor was not included in the models from the two later life-history stages because only juveniles that survived to 2 (Elo deviance at adulthood) or 3 (Elo deviance after first year of adulthood) were included in these models. Elo deviance in all models was coded as a categorical predictor with two categories: above average deviance and below average deviance (average deviance was assessed relative to their peers). Models with Elo deviance as a categorical predictor performed better than the same models with Elo deviance as a continuous predictor, and in all cases where the categorical predictor was significant, so too was the continuous predictor.

Modeling lifetime reproductive success

We used Poisson Generalized Linear Models to assess the effects of Elo deviance calculated at the three life-history stages on lifetime reproductive success (LRS). LRS was calculated for the subset of the juveniles that were female and had died during the study (n = 100). We could not assess LRS for males because they dispersed and because we could rarely determine which male sired which offspring. LRS was calculated as the number of offspring surviving to adulthood produced by each individual. We included the same predictors in our models of LRS as we included in the survival analyses.

RESULTS

General patterns of rank acquisition

Variation in Elo deviances binned by month of age declined steeply (β = -2.995 ± 0.614) until just after the first year of life (break-point = 13.25 months; Davie's test p <

0.0001), after which it increased gradually (Figure 4.1). Examination of individual Elo deviance scores assessed relative to their peers at the three different life-history stages shows a similar pattern. The standard deviation of Elo deviance at den independence (sd = 62.937, mean = -0.771, n = 465) was around double the standard deviation of Elo deviance at onset of adulthood (sd = 32.655, mean = 0.210, n = 384) and after the first year of adulthood (sd = 32.753, mean = -4.223, n = 208). Importantly, the highly variable Elo deviance at den independence reflected variability in the process of maternal rank inheritance, but not deviation from that process. Ultimately, most juveniles typically acquired their rank as predicted by maternal rank inheritance with youngest ascendency, regardless of their Elo deviance at den independence (Figure 4.2). Rank at the onset of adulthood was highly correlated with the mother's rank in that year (Pearson's r = 0.980; 95% CI = [0.970, 0.986]; n = 100), and 77% of new adults acquired their rank exactly according to maternal rank inheritance with youngest ascendency. A Chi-squared test revealed that Elo deviance class (above average or below average) did not predict whether juveniles acquired a rank above expected, below expected, or exactly as expected according to maternal rank inheritance with youngest ascendency (χ -squared = 1.518, df = 2, p = 0.468).



Figure 4.1. The timing of the development of juvenile social status. Piecewise linear regression revealed that juvenile Elo deviances were highly variable up until 13.25 months (dotted line), after which their variability was comparable to that of adults. This estimate of the timing of the establishment of social status resembles the 18 months (dashed line) described previously [Smale 1993].



Figure 4.2. In this study, 77% of juveniles acquired the exact rank predicted by maternal rank inheritance with youngest ascendency. Elo deviance at den independence (color) did not affect the rank attained at onset of adulthood.

Fitness correlates of Elo deviance at den independence

Elo deviance at den independence significantly predicted survival (n = 465; **Figure 4.3**): Juveniles with below average deviance scores at den independence showed increased mortality over the course of their lives (hazard ratio = 1.692; 95% CI = [1.256, 2.278]; p = 0.0005). Low maternal rank (hazard ratio = 1.380; 95% CI = [1.028, 1.853]; p = 0.032) and death of the juvenile's mother prior to reaching adulthood (hazard ratio = 2.144; 95% CI = [1.545, 2.976]; p < 0.0001) predicted reduced mortality. When Elo deviance was coded as a continuous predictor, it still predicted reduced mortality for higher deviances (hazard ratio = 0.866; 95% CI = [0.755, 0.994]; p = 0.041), but this model was not as good as the model with Elo deviance as a categorical predictor (Δ AIC = 8.001). Although Elo deviance at den independence was significantly correlated with Elo deviance at adulthood (Pearson's r = 0.194; 95% CI = [0.096, 0.289]; p = 0.0001, n = 208) and after the first year of adulthood (Pearson's r = 0.144; 95% CI = [0.008, 0.275]; p = 0.038), models with Elo deviance assessed at these later life-history stages did not predict survival (Elo deviance at adulthood: n = 384; Likelihood ratio test statistic = 6.15; p = 0.105; Elo deviance after first year of adulthood: n = 208; Likelihood ratio test statistic test statistic = 0.55; p = 0.907).



Figure 4.3. Survival probability as a function of Elo deviance at den independence and maternal rank. Juveniles with below average Elo deviance showed reduced survival, as did juveniles born to low ranking mothers. Death of the mother before the juvenile reached adulthood also predicted reduced survival (not depicted).

Elo deviance at den independence also predicted LRS (**Figure 4.4**); females with below average deviance at den independence produced fewer offspring than did females with above average deviance ($\beta_{Elo \ deviance \ below \ average} = -0.693 \pm 0.176$, p < 0.0001). Maternal rank had a strong effect on LRS ($\beta_{Low \ maternal \ rank} = -1.150 \pm 0.212$, p < 0.0001), and so did the mother's death before the juvenile reached adulthood ($\beta_{Mother died}$ = -1.038± 0.326, p = 0.0015). In similar models, Elo deviance class calculated at onset of adulthood marginally predicted LRS ($\beta_{Elo deviance below average} = 0.391 \pm 0.211$, p = 0.064) and Elo deviance class calculated after the first year of adulthood was a significant predictor of LRS ($\beta_{Elo deviance below average} = -0.392 \pm 0.173$, p = 0.023).



Figure 4.4. Lifetime reproductive success (LRS) as a function of Elo deviance at den independence and maternal rank. Juveniles with below average Elo deviance showed reduced LRS, as did juveniles born to low ranking mothers. Death of the mother before the juvenile reached adulthood also predicted reduced LRS (not depicted).

DISCUSSION

Our results have revealed that although rank acquisition follows a very

predictable pattern of maternal rank inheritance with youngest ascendency in spotted

hyenas (Figures 4.1, 4.2), this process varies considerably among individuals, and this

variation has serious consequences for both survival (Figure 4.3) and reproductive

success (**Figure 4.4**). Individuals who tended to lose to their lower-born peers during the den dependent period (thus incurring an Elo deviance below the average for their peers) suffered increased mortality and reduced reproductive success compared to those who did not. This study presents three important points.

The first is that the Elo deviance method introduced here has proved to be a powerful tool for measuring deviation from a hypothesized pattern of contest outcomes. It's ease of implementation, customizability for different questions, applicability to with any hypothesis makes this a valuable new tool in studying animal dominance structures. For example, here we used this method in two subtly different ways to ask slightly different questions about the ontogeny of dominance. We assessed variation in Elo deviance assessed relative to all other group mates at different ages to study the timing of the ontogeny of dominance, and found that maternal rank inheritance process was largely completed by 13.25 months old (a result similar to the 18 months identified in a previous study of the same population [26]). We also assessed Elo deviance scores relative to peers at three life-history stages to measure the consequences of variation in the process of maternal rank inheritance.

Second, our results demonstrate that the ontogeny of dominance is related to fitness in ways that are not explained simply by the social status that juveniles attain as adults. Here we found that the state of rank acquisition at den independence predicted survival and reproduction (**Figure 4.3**) but did not predict variation in the rank attained as adults (**Figure 4.2**). This result suggests that studies that focus on social status in adulthood overlook important potential rank-related influences on fitness that occur during development.

Finally, our results add support to the growing literature on early life conditions suggesting that hardship endured early in life can have profound and long-lasting consequences. Social defeat and social uncertainty in dominance relationships has been shown to incur costs [32–34]. Here, juveniles that were defeated by peers that they would eventually come to dominate showed reduced survival and impaired reproductive success, suggesting that social uncertainty coupled with social defeat could be a source of early life adversity in spotted hyenas. Our results are consistent with this suggestion. If we recode the three significant predictor variables (Above/below average Elo deviance at den independence, High/low maternal rank, Mother alive/dead when juvenile reaches adulthood) into a single variable that counts the number of adverse conditions experienced by each juvenile, the number of early life adverse conditions significantly predicts increased mortality (hazard ratio = 1.746; 95% CI = [1.434, 2.127]; p < 0.0001; Figure 4.5). These results demonstrate that the adverse conditions studied here have cumulative effects, in that juveniles experiencing multiple adverse conditions suffer the additive combination of the consequences of each. In some species [35], multiple sources of early life adversity have compounding effects, in which the combination of sources of adversity have more severe consequences than the summation of the independent effects of each. We did not find any evidence for compounding effects here: the model with number of adverse conditions did not perform better than the original model that included each source of adversity as a separate fixed effect (AICc = 0.114), and a model including interactions between the adverse conditions performed more poorly than the model without interactions ($\triangle AICc = 5.394$).



Figure 4.5. Survival probability as a function of the number of adverse conditions faced by juveniles during early life. The adverse conditions considered here were below average Elo deviance at den independence, low maternal rank, and death of mother before reaching adulthood.

In our future work, we intend to investigate potential causes of the variation in rank acquisition we document here using fine-scale studies of the behavior of developing juveniles and their kin. Here, we were unable to determine the causes of variation in rank acquisition. For example, variation in rank acquisition could be due to intrinsic differences between juveniles in quality or temperament. The fact that measures of rank acquisition calculated independently at different life-history stages were correlated is consistent with this conjecture. However, prior studies in spotted hyenas and other species with nepotistic societies suggest that mothers and other kin play an important role in the rank acquisition process, so the variation we observed here could also be sensitive to the behaviors of kin. In our future work, we will examine finescale changes in Elo deviance in conjunction with the behavior of juveniles and their relatives.

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