

# Dominance behaviour of female vampire bats

*(Desmodus rotundus)*

Submitted by Rachel Crisp to the University of Exeter as a dissertation for the  
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## Abstract

Female vampire bats (*Desmodus rotundus*) are a model for the study of cooperation in behavioural ecology, but we know very little of their conflict. This gap in knowledge is surprising given that competition over resources, and thus conflict, is an expected consequence of group living (Clutton-Brock & Huchard, 2013). Further, it is important to understand how vampire bats compete and resolve conflict because there is evidence to suggest that patterns of conflict are associated with patterns of cooperation (e.g. Schino & Aureli, 2008). We aimed to address this gap by observing competitive interactions occurring over food within a captive colony of 33 vampire bats which included adult females and their young aged 5 months and younger. To understand whether there was a pattern to competitive interactions we looked for evidence of a dominance hierarchy. We found strong evidence for a weakly linear dominance hierarchy, tested using three standard metrics: directional consistency, Landua's  $h'$ , and triangle transitivity. Randomised Elo-ratings showed that the hierarchy was not steep. We also found no evidence that rank was predicted by body size, sex, age, reproductive status, social group origin, or kinship. Taken together, these results strongly indicate that vampire bat social interactions are predominantly egalitarian. To put our results in a broader context, we compared dominance hierarchy metrics in female vampire bats to 172 published datasets from other taxa. Female vampire bat dominance was less linear and less steep than over 95% of other taxa. This indicates that female vampire bats are exceptional in their lack of a strict dominance hierarchy. Our results are consistent with the prediction that egalitarian or low-sloped hierarchies will occur in species characterised by symmetrical and reciprocal cooperative relationships which supports the biological market theory of cooperation.

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## Chapter 1 - Literature Review

*“There is more to dominance than simply the question of who eats the leaves.”*

*Frans de Waal*

Social living is widespread among mammals and has important fitness consequences. There are a number of ways in which living in groups is beneficial for group members (reviewed in Krause & Ruxton, 2002; Rubenstein & Abbot, 2017). One benefit is increased protection from predators. For instance, some studies have demonstrated that individuals that aggregate together may be more effective at avoiding predators because due to increased group vigilance (van Schaik, 1983), mobbing (van Schaik, 1983, Sterck et al, 1997) or by the dilution of individual risk (Pitcher & Parrish, 1993). Another, not necessarily mutually exclusive, benefit to individuals afforded by group living is increased resource acquisition or defence: Those in groups may have greater foraging efficiency because they are able to spend less time being vigilant and more time foraging (Elgar, 1989) or because those in groups are able to cooperatively defend high-quality food patches from other groups (Wrangham, 1980, Janson & van Schaik, 1988). In addition, group living may also confer other benefits such as cooperative rearing off offspring (Hatchwell & Komdeur, 2000) and increased access to mating opportunities (see Majolo, Huang & Lincoln, 2018).

However, group living is costly because it almost inevitably leads to increased competition for resources such as food, mates and space (Clutton-Brock & Huchard, 2013; Janson & van Schaik, 1988; Krause & Ruxton, 2002). Resource competition is costly for two main reasons. Firstly, lack of resources has important consequences on lifetime reproductive fitness. For instance, lack of food can

reduce the reproductive success of female mammals (Lee, 1987; Janson & van Schaik, 1988). Secondly, competition is energetically costly because it can lead to physical conflict that causes injury or death (Drews, 1996).

When individual differences in competitive ability exist among groupmates, weaker individuals may wish to sacrifice resource access in order to avoid conflict, and thus costly injury, with those that have superior competitive ability (Chase, 1982; Drews, 1993). One way members of a social group can maximise on the benefits of group living and minimise the costs of repeated and escalating aggression is by forming a dominance hierarchy (Drews, 1993; Sapolsky, 1993).

Dominance hierarchies were at first more heavily studied in male mammals. This was, at least in part, because of an early theoretical emphasis on male intra-sexual competition (see Clutton-Brock & Huchard, 2013). Classical sexual selection theory viewed intra-sexual competition as occurring primarily over mating opportunities in the sex with the greatest variance in lifetime reproductive success (LRS) (Bateman, 1948). Placental mammals are typically characterised by defence polygyny (Lukas & Clutton-Brock, 2013; Rutberg, 1983), in which a few males monopolise access to fertile females, leading to a greater variance in LRS among males than females (Bateman, 1948; Payne, 1979). It was therefore predicted that greater sexual selection upon traits that confer access to reproductive opportunities should occur in males rather than females (Andersson, 1994; Emlen & Oring, 1977). These traits can include weaponry or ornamentation (Dubuc, Ruiz-Lambides, & Widdig, 2014), which in turn may determine social rank. Even where there exists substantial secondary sexual characteristics among females, their role in intra-sexual competition has been overlooked in favour of alternative explanations such as male mate choice (Clutton-Brock & Huchard, 2013; see Watson & Simmons, 2010). A bias towards the study of rank in males may also be a reflection of the



relative ease to observe intra-sexual competition in males rather than females (Clutton-Brock & Huchard, 2013; Rosvall, 2011). For instance, it may be easier to distinguish polygynous males from one another through greater bodily scarring or secondary sex characteristics (Clutton-Brock & Huchard, 2013).

Studies of dominance in females is more common in species in which intra-sexual competition is overt. Social rank is a strong driver of behaviour among females of cooperatively breeding species, in which female reproductive skew can be very high (Clutton-Brock *et al.*, 2006; Hauber & Lacey, 2005). In these species, intense female intra-sexual competition can drive the development of exaggerated secondary sex characteristics, such as large body size, that confer competitive success (Clutton-Brock, 2009; Rubenstein & Lovette, 2009). Competition may [be](#) so intense that dominant females may even monopolise breeding by suppressing reproduction of subordinates. For instance, aggression from dominants is thought to increase stress hormone levels, leading to infertility in subordinates (Young *et al.*, 1996).

Even where evidence of competitive behaviour among females is not obvious, intra-sexual competition still occurs. Female plural breeders do not compete over access to mating opportunities because there is low reproductive skew (Clutton-Brock & Huchard, 2013). However, they do still compete over mate quality (Rosvall, 2011) and access to resources needed to reproduce well (Clutton-Brock & Huchard, 2013; Stockley, 2011; Stockley & Bro-Jørgensen, 2011). Indeed, competition and social rank is emerging as an important component of behaviour among plural breeders (Clutton-Brock & Huchard, 2013). Much of this work has primarily taken place in long term field studies of marked individuals. Of these studies, an increasing number demonstrate that, in addition to explaining patterns

of conflict, social rank is also important with respect to explaining patterns of cooperation (see Section 1.1).

Common vampire bats (*Desmodus rotundus*) are a textbook example of cooperation for their food sharing behaviour (Wilkinson, 1984). Vampire bats form strong cooperative bonds with kin and non-kin, with whom they allo-groom and share blood meals (Carter & Wilkinson, 2013, 2015; Wilkinson, 1984). There is strong evidence to suggest that the formation of these social bonds is associated with reciprocal sharing and kinship: starved bats are more likely to receive food donations from relatives or unrelated bats they have donated blood meals to in the past (Carter & Wilkinson, 2013). It is less known, however, whether female vampire bats compete over resources such as food, mates or space; whether they form a dominance hierarchy, and whether conflict, if any, influences their cooperation.

In order to address this gap, we aimed to conduct the first study of conflict and dominance in female vampire bats. In order to better understand the relationship between conflict and cooperation, we first review the literature of social rank in female diurnal old world primates where social rank and its influence on cooperation has been best studied: In these taxa we first discuss the 'socio-ecological' models that have been used to describe the causes of variation in dominance hierarchies and second, we discuss how rank is related to cooperation in the strictest of these hierarchies. To introduce the study system and outline the importance of studying social rank in them, we then overview the vampire bat social system and ecology. Then, to understand how dominance is studied, we review the methods that are commonly used to infer dominance hierarchies.

## 1.1. Social rank in female primates

Although nonhuman primate social systems are widely variable, the vast majority of diurnal species may be characterised by female gregariousness (Sterck, Watts & van Schaik, 1997). According to Emlen & Oring (1977) female gregariousness occurs as a result of the distribution of food resources and the risk of predation, meanwhile male distribution is a result of the distribution of mating opportunities. Consequently, males should derive less fitness benefits from forming alliances since they will derive a greater benefit from excluding other males from the group and thus mating opportunities. Females, meanwhile, stand to derive benefits from the formation of alliances with other group members if it influences their access to food resources. Indeed, coalitionary relationships are common among old world diurnal primates (van Schaik, 1997). Socio-ecological models have been used to describe the causes and consequences of this pattern. According to this theory, females form associations in order to minimise predation risk (Janson, 1992) but the inevitable increase in competition over resources occurring within groups (van Schaik, 1983) and between groups (van Schaik, 1989) combined with how easily these resources can be defended (Wrangham, 1980) influences the form of social relationships among females to give rise to four types of social systems. Following Sterck, Watts & Schaik (1997), van Schaik (1989) and Wrangham (1980), these may be summarised as follows:

First, when there is low within-group and low between-group competition, resources should be distributed evenly meaning that there is little benefit to the formation of alliances. Consequently, females should disperse and their relationships should be egalitarian. Although it may be possible to identify some conflict or variation in winning, these 'ranks' should not have a strong impact on fitness. This type of group is known as 'non-female-bonded' or 'Dispersing-

Egalitarian'. Second, when there is low competition within the group but there is high competition between groups, we expect that females will be philopatric in order to avoid the costs of eviction or dispersal, or in order to reside with female relatives to cooperatively defend resources, but since there is little to gain from forming differentiated alliances or strong dominance relationships within the group, relationships should be egalitarian. This type of group is known as 'female-resident' or 'Resident-Egalitarian'. Third, when there is high within-group competition but low competition between groups, there is strong selection to form differentiated relationships within the group leading to female philopatry, alliances among kin and non-kin, as well as stable, nepotistic and highly linear dominance hierarchies. This type of group is known as 'female-bonded' or 'Resident-Nepotistic'. Fourth, when there is strong competition both between and within groups, we expect female philopatry and strong selection to form stable linear dominance hierarchies. Because high-ranking individuals are dependent on support from lower-ranked individuals in between-group contests, we expect greater tolerance within-group since high-ranking individuals may risk the loss of support if they limit lower-ranked individuals access to resources too strongly (van Schaik, 1989). This type of group is known as 'tolerant female-bonded' or Resident-Nepotistic-Tolerant. With some exceptions, this theory is well supported in primate species however there has been some difficulty in measuring between group competition which limits how well the model can be tested and it has also been highlighted that female gregariousness may also be influenced by other factors including risk of infanticide and habitat saturation (see Sterck, Watts & van Schaik, 1997).

The causes and consequences of dominance hierarchies have been particularly well studied in the old world primates rhesus macaques (*Macaca*

*mulatta*) and baboons (*Papio* sp.). Rhesus macaques and baboon females form highly stable, and strongly linear dominance hierarchies (Bernstein & Williams, 1983; Silk, Seyfarth, & Cheney, 1999) with distinct hierarchical relationships between each individual and between each matriline (Maestriperi & Hoffman, 2012; Sade, 1967; Silk *et al.*, 1999). Social rank is important because it correlates with proxies of fitness in these species. For instance, higher ranking macaques mature earlier (Sade, 1976), live longer (Blomquist, Sade, & Berard, 2011; Brent *et al.*, 2017) and have higher rates of infant survival (Blomquist *et al.*, 2011). Similarly, higher ranking baboon females produce more offspring and reproduce sooner (Altmann & Alberts, 2003).

In addition to social rank, social bonds are also an important feature of baboon and rhesus macaque sociality and fitness. Both species form social bonds that are not only highly differentiated but are also apparently evolutionarily adaptive. Social connections in rhesus macaques are linked to greater longevity (Brent *et al.*, 2017), higher offspring survival (Brent *et al.*, 2013) and lower physiological stress (Brent *et al.*, 2011). In baboons, social bonds are associated with longer lifespans (Silk *et al.*, 2010), as well as increased offspring survival (Silk *et al.*, 2009), reproductive success (Silk, Alberts, & Altmann, 2003) and birth rate (McFarland *et al.*, 2017). Further, indirect social network ties are also important in these systems. Female baboons and rhesus macaques that form bonds with other well connected females have higher sociality index and have greater offspring longevity (Brent *et al.*, 2013; Cheney, Silk, & Seyfarth, 2016).

The strongest predictors of between which individuals social bonds occur are kinship and social rank. Female primates form their strongest relationships with their closest kin (Call, Judge & de Waal, 1996; Kapsalis, 2003; Silk, Altmann, & Alberts, 2006), with whom they groom more than non-kin (Silk *et al.*, 1999; Wu *et*

*al.*, 2018). In addition, they form many weaker social bonds with non-kin, which are influenced most by dominance rank (Kapsalis, 2003). For instance, when both baboon and rhesus macaque females form non-kin relationships, typically it is with those of a similar rank to themselves (Seyfarth, Silk, & Cheney, 2014; Silk *et al.*, 2006; Snyder-Mackler *et al.*, 2016; Thierry *et al.*, 2008). Moreover, when kin are absent, social rank is the strongest predictor of social bond formation in rhesus macaques (Snyder-Mackler *et al.*, 2016). There two main models used to explain the relationship between social rank and social bond formation: Seyfarth's "grooming for support" model (1977) and Henzi & Barrett's "biological market theory of grooming" model (1999).

Seyfarth (1977) proposed that rank may influence the formation of social relationships if cooperative behaviours, such as allo-grooming, may be exchanged for rank related services such as coalitionary support. Since high ranking individuals can provide more effective coalitionary support (Schino & Aureli, 2008), lower ranked individuals should prefer to form grooming relationships with those of a higher rank. In this sense, if low ranked individuals form affiliative relationships with high ranked individuals, they may be able to overcome some social and ecological limitations imposed by their rank. The partner choices available to each member of a group should, however, be constrained by competition for highly ranked partners. Consequently, Seyfarth (1977) predicted that high ranking individuals should receive the most grooming and relationships should form more often between adjacently ranked females due to competition. These predictions were supported by a meta-analysis of 14 species of primates, which found that grooming networks were strongly influenced by an attraction to kin and high ranking partners, and competition over high ranking grooming partners (Schino, 2001). A later meta-analysis also found evidence for a positive correlation between grooming and

coalitionary support in 36 groups from 14 species (Schino, 2007). Some authors, however, have argued that the 'grooming for support' hypothesis is limited since species such as female chacma baboons engage in reciprocal grooming relationships but do not form coalitions (Henzi *et al.*, 1997).

Alternatively, Henzi & Barrett (1999) agree that rank may influence social bonds due to the trading of cooperative goods, but hypothesise that social rank and social bonds should interact differently depending on the steepness of the hierarchy. The authors relate primate grooming patterns to a biological market (Barrett & Henzi, 2001; Noë & Hammerstein, 1995) in which grooming represents a commodity that can be reciprocally traded for grooming itself, or interchanged for alternative goods, such as tolerance. The market value of goods and which individuals can offer them, however, depends on the degree of intraspecific competition occurring with the group. In very steep hierarchies where access to resources, such as feeding sites, is determined by social rank, intraspecific competition is intense. In such scenarios, low ranked individuals stand to benefit from gaining a close association with higher ranked individuals if their affiliation translates to increased tolerance at feeding sites (Barrett, Gaynor & Henzi, 2002). Affiliative behaviours such as grooming may thus be 'exchanged' for tolerance from high ranked individuals. The greater the difference in social rank, the more valuable the partnership. Consequently, steep hierarchies should have a greater number of "interchange groomers", whereby grooming is directed up the hierarchy. In contrast, when resources cannot be monopolised and/or when dominance relationships are shallow, individuals are not able to offer rank limited commodities because there is less of a power differential between the highest and lowest ranked individuals. A greater proportion of relationships in shallow or egalitarian hierarchies should thus be "reciprocal trades" since grooming can only be exchanged for itself. This theory

has received some support in chimpanzees (*Pan troglodytes*) (Kaburu & Newton-Fisher, 2015) and bonobos (*Pan paniscus*) (Stevens *et al.*, 2005). One study also found of bonobos and chimpanzees found that as despotism increased, grooming reciprocity decreased (Jaeggi, Stevens & van Schaik, 2010). Schino & Aureli (2008) also found within-species evidence for an association between hierarchy steepness and the degree of reciprocation from a meta-analysis of 38 groups from 13 primate genera. The authors found that while reciprocity dominates in shallow hierarchies, the value of rank related currencies, such as tolerance or agonistic support, is positively correlated with the steepness of the hierarchy.

Both Seyfarth's 'grooming for support' model (1977) and the biological market model of primate grooming (Henzi & Barrett, 1999) predict that reciprocal affiliative relationships should be most common in pairs of animals that are similar in rank. Each propose alternative mechanisms behind this pattern, however. The Seyfarth model predicts that grooming relationships should be limited to those that are similar in rank as a consequence of competition occurring over high value partners. The biological market model, meanwhile, predicts that grooming should be well distributed among dyads and that individuals should be able to maintain multiple relationships that may be characterised as 'interchange' or 'reciprocal'. The type of relationships should, in turn, depend upon the steepness of the hierarchy: When there is a greater rank distance between partners and a steeper power gradient, there should be a greater inequality in grooming behaviour (Barrett & Henzi, 2001).

Other socially complex taxa are subject to similar socio-ecological influences on group dynamics and indeed, associations between social rank and the formation of social bonds have been identified in these cases. For instance, the distribution of food resources influences female gregariousness in carnivores (Pusey & Packer,



1987; Packer & Ruttan, 1988). Similarly to baboons and rhesus macaques, female spotted hyenas preferentially form social bonds with those that are higher or adjacent in rank to themselves (Smith, Memenis & Holekamp, 2007). In contrast, although some group-living ruminants form strict linear dominance hierarchies that influence reproductive success, there is no evidence that rank is inherited or that it is related to female philopatry (see Sterck, Watts & Schaik, 1997). It may therefore be possible that the covariance in food distribution, within- and between-group competition, dispersal and dominance hierarchies as formulated by socio-ecological models may be limited in explaining socio-ecological patterns outside of primates. Nevertheless, a number of other animals, such as dolphins and African elephants (reviewed by Seyfarth & Cheney, 2012), also form cooperative social bonds. It is thus possible that formation of social bonds in these animals is also influenced by social rank but we do not yet know.

## 1.2. Vampire bats – *Desmodus rotundus*

Common vampire bats (*Desmodus rotundus*) are New World leaf-nosed bats (family: Phyllostomidae) found in the American neotropics (Wetterer, Rockman & Simmons, 2000). They are highly social; forming large fission-fusion colonies ranging from less than 10 individuals to 300, although in some rare instances, colonies in excess of 2,000 individuals have been observed (Arellano-Sota, 1988; Flores-Crespo & Arellano-Sota, 1991). Roosts are used throughout the day; vampire bats typically only emerge at night when they leave to feed exclusively on the blood of large animals such as capybara, deer, peccaries, tapir and humans but most often livestock including horses and cattle (Mayen, 2003; Schmidt, 1995; Voigt & Kelm, 2006). For example, in one study, over 90% of vampire bats sampled had fed on domestic livestock (Campos-Vela, 1972).

Roosting colonies are comprised of smaller groups of 8-12 adult females and their offspring (Wilkinson, 1985a). Males disperse between 12 and 18 months of age (Wilkinson, 1985b) and, as adults, are more often observed to roost alone and switch roosts than females (Wilkinson, 1985a). Within each roost there is typically a small group of so-called 'resident' males which form a dominance hierarchy (Wilkinson, 1985b). Associations between males are typically agonistic; males in trees actively and often, aggressively, defend a position within the roost (Wilkinson, 1985a; 1985b). Males who successfully defend the highest position in the roost, where females are more often located, copulate the most and sire the most offspring (Wilkinson, 1985b). Males occupying lower positions in the roost copulate less, sire less offspring and are rejected more frequently by females (Wilkinson, 1985b). There is also some evidence that non-resident males visit female roosts and potentially mate (Wilkinson, 1985a). There is no evidence to suggest that females compete for access to males. On average, males at the tops of trees maintain their position for 12 months (Wilkinson, 1985b). Tenure is typically ended when aggressive interactions between males result in a new male taking the 'top' position in a roost and the previous dominant male permanently leaves the roost (Wilkinson, 1985a).

Females, meanwhile, are matrifocal and roosting groups are typically comprised of multiple matrilineal groups (Wilkinson, 1985a) and relatedness within groups is on average between 0.02 and 0.11 (Wilkinson, 1985b). Female roost-mates form strong and stable relationships, often roosting together for 10 years or more (Wilkinson, 1985a). These relationships are typically affiliative and are characterised by social grooming which occurs both between kin and non-kin females (Wilkinson, 1984; Carter & Wilkinson, 2013; Carter & Leffer, 2015). In fact, allogrooming is more common in vampire bats than any other species of bat

(Wilkinson, 1986; Carter & Leffer, 2015). Interestingly, allogrooming is not strongly associated with the removal of ectoparasites (Wilkinson, 1985a; 1986). Instead, allogrooming is theorised to serve social functions in relation to the formation and maintenance of social bonds and cooperative food sharing (Wilkinson, 1986).

Adult female vampires also regurgitate blood meals to both kin and non-kin that have been unsuccessful in foraging (Wilkinson, 1984; Wilkinson, 1985a; Carter & Wilkinson, 2013; Delpietro *et al.*, 2017). Being obligate blood feeders with a poor capacity for fat storage (Freitas *et al.*, 2013), starvation can occur as rapidly as 72 hours following the failure to obtain a blood meal, and unsuccessful foraging occurs as often as 33% of nights in bats less than 2 years of age (Wilkinson, 1984). Food donations are therefore vital for female fitness, and donation rates are driven by kinship, social bonding and prior history (Wilkinson, 1984; Carter & Wilkinson, 2013). This cooperative food sharing behaviour is considered to be a strong driver to the formation of long-term social bonds and colonies: Wilkinson (1985a) indicated that there is not strong evidence that vampire bats form social groups in order to avoid predators or parasites, to have better access to prey, to defend against coercive males or as due to lack of available roost sites with a suitable microclimate.

Females within a group do not appear to compete for access to roosts, but they might compete for food. Schmidt & van de Fliedrt (1973) observed captive bats aggressively interacting for access to blood, and Greenhall, Schmidt & Lopez-Forment (1972) found evidence of an order of feeding at feeding sites in the wild. In a captive group of 9 vampire bats males appeared submissive to females (Park, 1988) and similar anecdotal observations have been made in wild bats (Delpietro *et al.*, 2017). As of yet however, there has been no study to assemble a dominance hierarchy using methods commonly used in primates.

It is important to gain an understanding of whether social rank plays a role in vampire bat social behaviour and the formation of social bonds for several reasons. For one, although there is strong evidence that reciprocity and kinship play substantial roles in the formation of social bonds, there is still some variation in bond formation that cannot be explained by these factors alone (Carter & Wilkinson, 2015). Since dominance is known to play a large role in bond formation in primates and other species, it is possible that dominance rank could explain this variation. Second, recent studies consider the relative roles of kinship and reciprocity in the social bond formation (e.g. Carter & Wilkinson, 2013). In such studies, without an understanding of the role of social rank, it is possible that the relationship between reciprocity, kinship and bond formation may be misunderstood. Further, there is some evidence to suggest that the effect of social rank may be stronger when kin are absent (Snyder-Mackler *et al.*, 2016). Recent studies of vampire bat behaviour are often conducted in captivity (e.g. Carter & Wilkinson, 2015). It is possible that social rank, if important, may play an even stronger role in captivity if less kin are present. If this is the case, without an understanding of social rank in vampire bats, our ability to understand the relative roles of kinship and reciprocity in the formation of social bonds may be further complicated.

Further, vampire bats make an interesting comparison with old world primates for two reasons. Firstly, despite their ancestors having diverged more than 70 million years ago (Lin & Perry, 2001), common vampire bats share many convergent social traits with primates including female philopatry with multiple matrilineal lines (Wilkinson, 1974), long lifespan (30+ years in vampires), periods of offspring dependency (>1 year), social grooming, and the formation of complex social bonds between kin and non-kin (Wilkinson, 1984; Carter & Wilkinson, 2013; Carter & Leffer, 2015). In comparison to other bats, vampires are outliers for both

social complexity (Carter & Leffer, 2015) and relative neocortex size (Baron *et al.*, 1996; Bhatnagar, 2008). Despite these similarities in life histories, we know very little about female dominance hierarchies in vampire bats. Secondly, studying cooperation and conflict in vampire bats has several advantages over old world primates. Costly helping behaviours such as food sharing are rare and difficult to induce in primates (Jaeggi & Gurven, 2013), yet are measurable and easy to control in vampire bats. Food sharing provides a window into understanding social relationships because it is easily induced, measured, and manipulated by selectively starving individuals (Carter & Wilkinson, 2013). This allows for faster data collection and greater control compared to passive observations of natural cooperative behaviours in primates.

Despite many parallels between female social bonds in primates and vampire bats, and considering the depth of focus on cooperation in vampire bats, it is surprising that we know nothing of female conflict, specifically whether competition over food leads to the formation of a social dominance hierarchy. This gap presents an opportunity to compare the role of female rank and cooperation with what we know from primate studies, and to enrich our understanding of vampire bat cooperation.

### 1.3. Measuring dominance

The study of dominance comprises a multitude of different methods and metrics that characterise a variety of different components of dominance-related social structure. There is not a standardized method for inferring hierarchies particularly in cases where it is not known prior to study whether a hierarchy does or does not exist. Broadly speaking, dominance measures may be classified into

three classes. First, those that characterise the overall structure of a dominance network, and second, those that assign individual rank orders to members of a social group. The third group consists of metrics that may be used to determine how confident one can be that an observed hierarchy is accurate. Below, I describe each of these features of dominance hierarchies, and the methods used to quantify them, in more detail.

### 1.3.1. Overall dominance structure

As formalized by Drews (1993), dominance may be defined as “an attribute of the pattern of repeated, agonistic interactions between two individuals, characterized by a consistent outcome in favour of the same dyad member and a default yielding response of its opponent rather than escalation”. As a result, dominance interactions are expected to exhibit two key criteria (van Hooff & Wensing, 1987). First, dominance interactions should be linear, whereby a dominance relationship exists between all dyads within a social group. Linearity may be expressed as transitivity, meaning that for any given triad within the group, if A dominates B and C, B should dominate C, and C should perform dominant behaviour towards neither B or A. By definition, the greater the number of triangles that are intransitive, the less linear the hierarchy (Chase, 1982). Linearity or transitivity may be quantified via Laudau’s modified  $h'$  index (de Vries, 1995) or triangle transitivity (Shizuka & McDonald, 2012). Second, dominance interactions within each dyad should be asymmetrical, i.e. more commonly directed by one individual towards the other. The degree of asymmetry in relationships may be quantified via a ‘Directional Consistency Index’ (van Hooff & Wensing, 1987). Hierarchies may also differ in the power differential between members of the group,

which may be characterised through measures of hierarchy steepness (e.g. see McDonald & Shizuka, 2013).

#### 1.3.1.1. *Landau's modified $h'$ index*

The  $h'$  index is an improvement on Landau's  $h$  index (Landau, 1951) devised by de Vries (1995). The original metric,  $h$ , measures the degree to which transitive dominance relationships exist between all members of a group. An  $h$  value of 1 indicates that, within all dyads, dominant behaviours are performed more frequently by one member, while an  $h$  value of 0 indicates that all individuals dominate others equally. However, this method performs poorly when there are a large number of dyads that never interact, or that perform an equal amount of dominance behaviours to one another (Appleby, 1983), as is often the case. The modified metric,  $h'$ , overcomes these limitations by using a procedure to both correct  $h$  for the number of 'unknown' interactions and to determine whether interactions are stronger than expected by chance by comparing observed values to that of 1000 randomly filled matrices (de Vries, 1998; de Vries, 1995). A problem with this method is that 'unknown' interactions are corrected by being filled randomly. This leaves  $h'$  vulnerable to effects of group size or high proportions of dyads with an unknown interaction which may lead to underestimations of linearity or difficulties detecting a significant linear hierarchy (Shizuka & McDonald, 2012).

#### 1.3.1.2. *Triangle transitivity*

Triangle transitivity, or ' $T_{tri}$ ' index, characterises dominance structure by measuring the proportion of triads in which interactions are 'transitive' rather than 'cyclic'. To calculate  $T_{tri}$ , the proportion of transitive triangles in the network ( $P_t$ ) is divided by 0.75, the proportion of transitive triangles found in random networks, to

give a scale ranging from 0 to 1, in which 1 indicates all triads are transitive and 0 indicates all triangles are circular. This method is particularly robust when faced with variation in group size because it avoids the introduction of artefacts through imputation because absent values are not filled (Shizuka & McDonald, 2012). This is especially important if null dyads are prominent in a hierarchy. Consequently,  $T_{tri}$  can lead to more accurate estimations of linearity than Landau's  $h'$ , especially for sparse datasets.

### 1.3.1.3. *Directional consistency*

The directional consistency index (DCI) measures the asymmetry of behaviours within a network by measuring the frequency a specific behaviour is performed in one direction, relative to the total number of time the behaviour is performed in both directions (van Hooff & Wensing, 1987). To illustrate by example: one may wish to take the DCI of biting behaviour among a group of monkeys. DCI is first estimated for each dyad. In a hypothetical dyad that interacted 220 times, 85% of bites were from monkey A to monkey B, while monkey B bit monkey A in 15% of biting interactions. DCI for this dyad is calculated by subtracting 0.15, the proportion of total bites performed in the least common direction ("L") from 0.85, the proportion of total bites performed in the most common direction ("H"). This value is then divided by the total number of interactions in the dyad to give a value ranging from 0 to 1, in which 0 indicates no asymmetry in the performance of a behaviour, and 1 indicates all behaviours were formed in one direction. In this example dyad, bites had a DCI of 0.7, meaning that it was moderately uni-directional. The DCI of the network is then calculated as the average value across all dyads.



#### 1.3.1.4. *Hierarchy steepness*

According to van Schaik (1989; see also Vehrencamp, 1983) hierarchies can be broadly classified as 'egalitarian' or 'despotic' depending on the distribution of access to resources. Despotic hierarchies are those in which dominance relationships are highly linear and resources are heavily skewed towards a small proportion of the group. Egalitarian hierarchies are those in which there are weakly linear dominance relationships and there is low skew in resource access. The difference between these classifications may be quantified by the hierarchy steepness, which refers to the gradient of individual rank differences between members of a group or the degree to which rank difference can predict the propensity to win a given interaction. Steep slopes, in which ranks are highly differentiated, are characteristic of despotic hierarchies. Meanwhile, shallow differences in rank are characteristic of egalitarian hierarchies. To estimate steepness, de Vries, Stevens & Vervaecke (2006) proposed using the slope of a line fitted to the relationship between normalised David's scores (see section 1.3.2.1 below) and the players ranked from highest to lowest. Using this approach, 0 indicates that relationships are completely unskewed and egalitarian, and 1 indicates that the group is made up of skewed, despotic relationships. Hierarchy steepness may also be quantified by measuring the repeatability of rank assignments across time points or in permuted datasets (Sánchez-Tójar, Schroeder & Farine, 2018). Steepness and repeatability may also be used as proxies for hierarchy certainty (see section 1.3.3 below).

#### 1.3.2. *Individual ranks*

Individual ranks can also be assigned using a number of methods all of which typically formulate rank orders by assigning scores to competitors according to the

outcome of dyadic interactions. Three commonly used methods to assign individual dominance rank are: David's score, Elo-rating & Glicko-rating. Each of these three methods are described in more detail below.

#### 1.3.2.1. *David's score*

David's score (DS) calculates individual rank by summing wins and losses for each individual scaled to the summed scores of their interaction partners (David, 1987) resulting in a continuous rank index for each individual within the study group. DS performs well in comparison to other methods. For instance, DS performed equally well as I&SI, another commonly used method which assigns individual rank orders by minimising relationships that are inconsistent with a linear rank order (de Vries, 1998; Vervaecke *et al.*, 2007; Neumann *et al.*, 2011). Gammell *et al.* (2003) highlighted that DS also performs better than Clutton-Brock's index (Clutton-Brock *et al.*, 1979), a similar matrix based dominance measure, because it is more stable to minor deviations in expected dominance interactions that could otherwise result in exaggerated increases or decreases in rank (David, 1987). One limitation is that DS assumes interactions occur independently from one another. If there are strong winner/loser effects, whereby an individual's likelihood of winning or losing is influenced by its prior competitive outcome, DS will not perform optimally (Gammell *et al.*, 2003; de Vries, 1995).

#### 1.3.2.2. *Elo rating*

Elo-rating calculates individual rank using a common numerical rating or 'starting score' for all individuals within a group that is updated following each competitive interaction to give a final 'score' or rank (Albers & de Vries, 2001; Elo, 1978). Ratings for each individual stand to increase or decrease depending on

whether interactions are won or lost. The amount by which ratings change depends on whether the outcome of an interaction was expected according to the distance in rank between the two opponents. If a given outcome is unlikely, for instance if a very low ranking individual were to win over a highly ranked individual, the ratings of both players change more than if an outcome was likely. The degree to which ratings change following each interaction is set by a constant, “K”, which can be adjusted to reflect the intensity of competitive interactions. At the end of a given study period, a social rank order can be obtained based on respective Elo-ratings of all players. If individuals share a similar Elo-rating they may be termed to have the same “class”, meaning that they have a similar competitive ability and have undecided dominance relationships. Dissimilar Elo-ratings indicate that there exists a clear dominance relationship within a dyad.

Neumann *et al.* (2011) highlight that Elo-rating has several major advantages over matrix based ranking methods such as DS. First, by calculating ranks based on the order in which they occur, rather than calculating ranks from summed win/loss matrices, Elo-rating is able to account for winner/loser effects. It can also be used to study and visualise temporal variation in rank, which is a particular advantage when hierarchical relationships are unstable or change frequently. Second, the performance of Elo-rating is unaffected if the group size or group composition changes within the study period. This means that unlike methods such as I&SI, Elo-rating can be used for groups as small as two. Likewise, unlike methods such as DS, Elo-rating can account for rank changes that occur as a result of immigration or migration because final ratings are not calculated according to the total number of individuals in the group. Lastly, Elo-rating results in interval data which can thus be analysed parametrically.

One major limitation of Elo-rating, however, is that because rank estimates are continually updated, they may be unreliable if there are strong temporal effects on rank. For instance, if ranks change frequently over time, Elo-ratings from two given time points may not correlate highly with one another. A modification of Elo-rating, 'Randomised Elo-rating' overcomes these limitations by forming a final rank order from the average ratings obtained across duplicated datasets (n=1000) in which the order of interactions is randomised (Sánchez-Tójar *et al.*, 2018).

A further limitation is that if there is no existing understanding of dominance relationships within a group, Elo-rating begins by allocating all players an identical starting score from which ratings diverge as interactions accumulate. This introduces a refractory period or 'burn in' period during which Elo-ratings are unreliable until enough observations have been recorded to reflect the true rank order. Without prior knowledge of a hierarchy's structure, it is impossible to determine the length of the burn in period *a priori* because it is influenced both by the number of interactions observed and the frequency with which individuals interact. This can be particularly troublesome if players interact infrequently, or if a hierarchy is not steep as the burn in phase may exceed the duration of the study (Newton-Fisher, 2017). Similarly, there are no clear methods that can be used to determine when the end of the burn in period has been reached. Newton-Fisher (2017) suggested that the end of the burn in phase may be determined by when the highest ranking individual obtains a stable rank trajectory. However, this can only work during periods when ranks are known to be stable, which may not always be the case and is difficult to detect *a priori*. Thus, without stable ranks, prior knowledge of dominance relationships, or a high frequency of interactions it may prove more effective to use matrix based ranking methods (de Vries & Appleby, 2000).

### 1.3.2.3. Glicko rating

Glicko-rating is an extension of Elo-rating that provides a method to assess the confidence that can be afforded to assigned ranks (Glickman, 1999). Following each interaction, the amount in which a player's score changes differs depending on their respective 'rating deviation' or standard deviation of their rank. Small ratings deviations indicate that we can be highly confident an assigned rank is accurate, meanwhile large ratings deviations indicate a low confidence. Ratings deviations are adjusted when players are observed to interact. Each time a player interacts, their ratings deviation decreases, because we may be more certain about their competitive performance and therefore rank. The 'decay' function causes ratings deviations to increase when players have not been observed to interact for long time periods, so that the longer a player has been absent, the less certain we can be about their respective rank or performance. Glicko-rating also differs from Elo-rating in that the points which are gained or lost following an interaction are not matched in both players. Points are instead adjusted according to a function of the dyad's difference in rating and their respective rating deviations.

### 1.3.3. Hierarchy reliability

When exploring dominance structure in a species in which dominance has not been studied previously, it is difficult to determine both the most appropriate individual ranking method to use and how accurate rank estimates might be. For instance, utilising a single method to assemble a rank order from a set of interaction data does not provide any insight into the reliability of the estimates. Previously, authors have attempted to determine the performance of particular methods by making comparisons with alternative methods (Neumann *et al.*, 2011; de Vries, 1998). The relative advantages and limitations of each individual ranking method

have been well explored (see above), but there is no single method that has been deemed applicable for all types of data. For instance, Elo-rating can be used to visualise temporal rank dynamics that would otherwise be obscured by matrix based models, such as David's score or I&SI. Yet, in scenarios where there is a strongly linear hierarchy, methods such as I&SI perform better (Neumann *et al.*, 2011). It is, however, impossible to know the structure of data in advance. Thus it may be advisable to employ the use of multiple individual ranking methods.

One structural property of the data that may influence the reliability of individual ranking methods is the steepness of the dominance hierarchy. Very steep hierarchies, in which high ranking individuals win all interactions, are highly detectable and repeatable, even with a low number of observations. In contrast, very shallow hierarchies, in which the outcome of competitive interactions is less predictable, are more difficult to detect, less repeatable across time, and more strongly influenced by the number of observations. Thus, quantifying the steepness of a hierarchy can provide information about how certain we can be that an observed hierarchy reflects the true underlying dominance structure.

Recently, Sánchez-Tójar *et al.* (2018) proposed that two methods used to quantify the replicability of rank estimates could be used as a proxy for hierarchy reliability. The first quantifies the repeatability of Elo-ratings obtained across replicated datasets in which the order of interactions is randomised to give a metric ranging from 0 to 1 (Nakagawa & Schielzeth, 2010). Elo repeatability values that exceed 0.90 indicate a very steep hierarchy, meanwhile values over 0.65 may indicate a hierarchy of intermediate steepness. The second, "repeatability by splitting" or  $r_s$ , represents the correlation between two halves of a dataset, also yielding a metric ranging from 0 to 1. Very steep hierarchies have  $r_s$  values that exceed 0.90, hierarchies of intermediate steepness have an  $r_s$  below 0.86, and very

flat hierarchies do not exceed  $r_s = 0.44$ . The higher the values of both measures, the steeper and more certain the hierarchy (Sánchez-Tójar *et al.*, 2018).

#### 1.3.4. Research study

The aim of this thesis is to establish whether female vampire bats form a dominance hierarchy. There is some evidence of dominance interactions in vampire bats (Park, 1988) but, as yet, there has been no study of social rank in female vampire bats using commonly used ranking methods. To determine whether female vampire bats form a dominance hierarchy, we use and compare a variety of methods (see section 1.2) in order to explore the various aspects of dominance structure.

## Chapter 2 – Research Study

### 2.1. Introduction

Dominance hierarchies are an influential component of mammalian social life. Increased competition within social groups leads to conflict (Clutton-Brock & Huchard, 2013). When differences in competitive ability may be established (Chase, 1982; Drews, 1993), individuals may be able to minimise the costs of repeated and escalating aggression (Sapolsky, 1993) by forming a dominance hierarchy. Viewing dominance from only this perspective, however, precludes the full extent of its role within social groups because dominance may also be associated with patterns of cooperation.

A growing number of studies from long term field studies of marked primates have shown that dominance rank influences partner choice and preference in cooperative contexts. Following kinship (Call *et al.*, 1996; Kapsalis, 2003; Silk *et al.*, 2003; Silk *et al.*, 1999; Wu *et al.*, 2018), social rank is the next strongest predictor of which pairs of individuals form a social bond. Individuals preferentially form bonds with others that have ranks that are similar or higher than their own (Kapsalis, 2003; Schino, 2001; Seyfarth *et al.*, 2014; Silk *et al.*, 2006; Snyder-Mackler *et al.*, 2016; Thierry *et al.*, 2008; Wu *et al.*, 2018). Several authors have proposed that individuals may prefer to form social bonds with those that are of a higher rank if a social association provides them with better access to rank-limited resources (Seyfarth, 1977; Henzi, 1999). For instance, grooming has been linked to coalitionary support in several primates (Borgeaud & Bshary, 2015; Matheson & Bernstein, 2000; Schino, 2007; Schino, Giuseppe & Visalberghi, 2009; Ventura *et al.*, 2006). These results demonstrate that in order to understand cooperation, it is important to understand social dominance. Social bonds occur in taxa other than primates



(Seyfarth & Cheyney, 2012); it is possible that social dominance also plays a role in their formation, maintenance, and function.

Female vampire bats (*Desmodus rotundus*) are a model for cooperation but we know comparatively little about whether they experience conflict. Among bats, female vampire bats spend more time allo-grooming than other species (Carter & Leffer, 2015) and are unique for their regurgitated food sharing behaviour (Wilkinson, 1984). Food sharing is critical for vampire bats because they regularly fail to feed in the wild (Wilkinson, 1984) and have a poor capacity to store energy (Freitas *et al.*, 2005). Females form strong grooming and food-sharing relationships both with kin and non-kin (Carter & Wilkinson, 2013; 2015; Wilkinson, 1984) and food-sharing rates among pairs of female bats are positively predicted by reciprocal sharing and kinship (Carter & Wilkinson, 2013).

Female vampire bats do not appear to compete for access to roosts, but records of agonistic interactions in feeding contexts suggests that dominance relationships may determine access to food. Greenhall, Schmidt & Lopez-Forment (1971) observed wild bats engaging in combat at wound sites. Multiple bats were observed to feed one-by-one from the same wound over a 3-hour period. Feeding bats aggressively defended their access to wound sites against approaches from other bats. These interactions consisted of pushing and fighting, sometimes with vocalisations. Feeding bats were either driven away by an intruding bat, or were able to successfully defend their position at the wound. Similar anecdotal observations were also made in wild bats (Delpietro *et al.*, 2017).

Park (1988) also observed aggressive interactions occurring over food in captive vampire bats. The author observed similar aggressive behaviours such as pushing and fighting, as well as submissive behaviours such as waiting for feeding bats to finish before approaching to feed. Young bats tended to engage in

aggressive behaviours more than adults and males were submissive to females. The most dominant individual always fed first, but other bats did not follow a clear feeding order. Although there appears to be dominance patterns to behaviours, no study to date has rigorously characterised the presence of a dominance hierarchy in female vampire bats. We also do not know whether social rank influences social relationships. Social bonds are important to female vampire bats, and social rank may play a role in structuring social bonds.

In this study, we aimed to establish whether female vampire bats form a dominance hierarchy. We recorded the outcomes of dyadic social interactions occurring near blood spout feeders among a captive colony of 33 vampire bats housed in Gamboa, Panamá. We tested whether dominance interactions could be characterised as exhibiting a dominance structure using three alternative measures: Landau's  $h'$  measure of linearity, directional consistency and triangle transitivity. We measured the steepness of the hierarchy using randomised Elo-rating. We also quantified the dominance ranks of individuals using three common measures: David's score, Glicko-rating and Elo-rating and tested whether individual rank was predicted by body size, age, reproductive status and location of origin. To contextualise our results, we compared our female vampire bat dominance hierarchy structure, steepness and repeatability to that of other species from a variety of taxa.

Despite their ancestors having diverged more than 66.5 million years ago (Meredith *et al.*, 2011), common vampire bats share several convergent social traits with many old world primates, including female philopatry, fission-fusion social dynamics (Wilkinson, 1985a; Wilkinson, 1985b), long lifespan (30+ years in vampires), prolonged offspring dependency (>1 year), social grooming, individual vocal recognition, and complex social bonds between kin and non-kin (Carter &

Leffer, 2015; Carter & Wilkinson, 2013, 2015; Wilkinson, 1984). Though vampire bats are known for their cooperation, they are not indiscriminantly cooperative: They form highly differentiated social bonds, which vary to some degree which currently cannot be explained by kinship alone (Carter & Wilkinson, 2015). Because of these convergent traits with old world primates, their formation of differentiated social bonds and because we anticipated that they would experience high within-group competition but low between-group competition, we predicted that vampire bats would have 'Resident-Nepotistic' group social dynamics and consequently a steep, linear and stable dominance hierarchy comparable to that of primates such as rhesus macaques or baboons. We predicted that rank would not be associated with body size or age since 'Resident-Nepotistic' hierarchies are typically inherited rather than determined by physical characteristics. Finally, we predicted that the vampire bat hierarchy would be strongly linear, steep and repeatable in comparison to other species.

## 2.2. Methods

### 2.2.1. Subjects

Subjects were 33 common vampire bats (*Desmodus rotundus*) housed in a 2.25m x 4.5m x 2.5m cage at the Smithsonian Tropical Research Institute in Gamboa, Panamá. The colony was comprised of adult females captured in Panamá from two distant sites: Las Pavas (n=6) or Tolé (n=18) approximately one year before this study began, and 4 male and 5 female juveniles born in captivity between June 3, 2016 and December 15, 2016. Bats were individually-marked using a unique combination of metal bands of four types (coloured, round, shiny, dull) on their forearms.

Between the hours of 18:00 and 11:00, bats were able to feed from a row of 3 to 10 spouted tubes of porcine or bovine blood on the floor of the cage. To prevent coagulation, we added 11g of sodium citrate and 4g of citric acid per ca. 4 litres of blood after collection from a local slaughterhouse. To keep blood from spoiling, we replaced blood with new freshly thawed or refrigerated blood each night between 23:00 and 24:00.

### 2.2.2. Data collection

From November 1, 2016 to January 31, 2017, each night we video recorded feeders using an infrared-illuminated surveillance camera from 17:30 to 08:30. There were 21 non-consecutive nights of data during in this period that were lost due to technological errors, which left 70 night of footage for analysis (1050 hours of video). We did not know in advance which behaviours may be the clearest indicators of social dominance in vampire bats. Definitions of dominance vary, but according to Drews (1993) an operational definition of dominance may be based

upon a “*consistent outcome in favour of the same dyad member and a default yielding response of its opponent rather than escalation*”. In a dyadic interaction, a winner may be identified as “*the contestant that expresses consummatory behaviour*” while the submissive or loser may be identified from a yielding response to an aggressive action by another individual. Commonly used behaviours to establish dominance/submission include ‘approach-retreats’ whereby one individual moves away or ‘retreats’ when approached by a conspecific, and ‘supplants’ whereby one individual takes over the physical position, such as at a food resource, of a conspecific (Drews, 1993; van Hooff & Wensing, 1987). Since dominance relates to resource access, studies typically determine social rank by observing these dyadic interactions when they occur over food resources. Expressions of dominance or submission are not limited to competition over resources. Once a dominance relationship has been established, expressions of rank may occur in outside of a competitive context. For instance, rhesus macaques communicate rank using formalized dominance gestures. Submissive displays such as teeth-baring may occur merely in response to an approach by a dominant, perhaps to decrease the likelihood of aggression (Maestriperi & Wallen, 1997). Previous studies of conflict in vampire bats identified behaviours occurring over food access including aggressive ‘broadside shoving’ whereby bats would push each other away using the sides of their bodies, and submissive actions such as ‘flying away’ whereby bats would leave food stations upon the approach of a conspecific (Park, 1988).

To characterise the dominance hierarchy, we identified “winners” and “losers” from five types of pairwise agonistic interactions at the feeders:

1. **Push intrude:** a feeding bat is replaced at the feeder by an intruding bat using physical contact. The intruder is the winner.

2. **No push intrude:** the same as “push intrude” but without physical contact.
3. **Push defend:** a feeding bat uses physical contact to maintain its position at the feeder following an approach by another bat. The defender is the winner.
4. **No push defend:** the same as “push defend” but without physical contact.
5. **Waiting:** A bat in view does not begin to feed until a feeding bat leaves the feeder. The waiting bat is the loser.

From these interactions we created win/loss matrices, in which the total number of wins made by each individual against each possible opponent were summed. To assess whether the different interaction types indicated a similar underlying dominance structure, we calculated Pearson’s correlation coefficient between the matrices of the win totals for each interaction type and tested significance using mantel tests (5000 randomisations) with R package ‘vegan’ (Oksanen *et al.*, 2018).

### 2.2.3. Sampling effort

The performance of individual ranking methods at inferring dominance rank increases with the ratio of interactions to individuals (Sánchez-Tójar *et al.*, 2018). To estimate whether we had a sufficient sample of observations, we conducted two tests recommended by Sánchez-Tójar *et al.* (2018). First, we calculated the mean ratio of interactions to individuals; from simulations, the authors recommend a ratio of 10-20 interactions to individuals to give the most reliable estimates for moderately steep hierarchies ( $r_s > 0.7$ ). Note that the authors also recommend that a higher ratio of interactions to individuals may be necessary for very shallow hierarchies. Second, we compared the mean proportion of dyads that were observed to interact

during our study period to the mean proportion we would expect to interact in a group of equal size if the likelihood of interacting followed a Poisson distribution (i.e. few individuals engage in many interactions and most individuals engage in few interactions) since count data usually follows this type of distribution (Zuur *et al.*, 2009; Sanchez-Tojar *et al.*, 2018). Researchers can conclude that sufficient sampling has been undertaken if the proportion of dyads observed interacting meets or exceeds the mean expected under a Poisson distribution.

#### 2.2.4. Characterising the structure of the dominance hierarchy

We calculated three commonly used metrics to characterise the overall structure of competitive interactions using R package 'compete' (Curley, 2016): directional consistency (van Hooff & Wensing, 1987), Landau's modified  $h'$  index (de Vries, 1995) and triangle transitivity (Shizuka & McDonald, 2012). Directional consistency (hereafter 'DCI') measures structure by measuring how 'directional' wins are within a group. If there is a strong dominance structure to competitive interactions, wins should be asymmetrical or 'directional', meaning that more dyads should be characterised by one member of a dyad winning more than the other. If a greater number of dyads win equally as much as one another, there is a less strong dominance structure to competitive interactions. Landau's modified  $h'$  index (hereafter ' $h'$ ') measures the degree to which competitive interactions are linear. Similar to DCI, Landau's  $h'$  compares how frequently one member of a dyad wins more than the other, relative to how frequently both win an equal number of times. Interactions are highly linear if a high number of dyads are characterised by one member of the dyad winning more than the other. Triangle transitivity (hereafter ' $T_{tri}$ ') determines the structure of competitive interactions by measuring how linear or transitive wins are within possible triads in the group. Interactions are highly linear

if a greater proportion of possible triads are characterised by transitive triangles (whereby A wins more over B, A & B win more over C and C does not win over A or B) rather than cyclic triangles (whereby A wins more over B, B wins over C and C wins over A). All three indices range from 0 (completely non-ordered) to 1 (completely ordered) and thus provide a measure of whether the interaction network is more ordered than expected by chance, and characterise the extent to which competitive interactions are linear.

When the underlying dominance structure is not known, it is necessary to determine whether behaviours observed constitute dominance behaviours (de Vries, 1998). As a further test of whether the types of interaction we identified were appropriate parameters of dominance and whether these interactions were performed in an orderly fashion consistent with a dominance hierarchy, we calculated all three measures of orderliness detailed above for each interaction type and for all interaction types combined.

#### 2.2.5. Assigning individual social ranks

To estimate the relative rank of each bat, we used three alternative methods: David's score (David, 1987), using the R package 'compete' (Curley, 2016), Glicko rank (Glickman, 1999) and Elo rank (Neumann *et al.*, 2011), using the R package 'PlayerRatings' (Stephenson & Sonas, 2012). To estimate the similarity of rank ordering across these ranking methods, we calculated Pearson's correlation coefficients between the rank orders generated by each method.

We were able to observe changes in rank trajectories over time using Elo-rating and Glicko-rating because they both continually update ranks following each dyadic interaction. To determine whether these rank trajectory plots revealed orderliness in the data, we also produced Elo and Glicko rank trajectory plots from



19 null data datasets and visually compared these to our 'real' data. These datasets were generated by taking 19 replications of our observed dataset, and randomly replacing the observed identities of winners and losers with randomised combinations of possible actors. We chose to produce 19 datasets for comparison because  $1/20$  is 0.05. Thus, if our plot is visually different from 19 other plots, it would indicate a 5% that such a plot could have been observed due to chance and we could then reject the null hypothesis.

#### 2.2.6. Hierarchy steepness and certainty

To determine whether the observed hierarchy was reliable, we used two methods from R package 'aniDom' which calculate the repeatability of rank estimates when calculated with Elo-rating (Farine & Sanchez-Tojar, 2017). First, using the function '*estimate uncertainty by repeatability*' we calculated the repeatability of randomised Elo-ratings across replicated datasets in which the order of interactions was permuted ( $n=1000$ ) to give a score ranging from 0-1. High values ( $>0.8$ ) indicate that individual ranks are highly repeatable independently of the order in which observed competitive interactions occur. Second, using the function '*estimate uncertainty by splitting*' we calculated the correlation of Elo-ratings obtained when calculated from two halves of the dataset to give an index ( $r_s$ ) in which values that exceed 0.5 indicate that the hierarchy is repeatable. The higher the values of both randomised Elo-rating repeatability and  $r_s$ , the more reliable the hierarchy. These reliability indices may also be used as a proxy for steepness because hierarchies are more repeatable the greater the steepness.

### 2.2.7. Predictors of social rank

To examine whether rank was predicted by body size, we fit general linear models with both body mass and forearm length (proxies for body size in bats) as predictors of rank. To assess whether vampire rank correlated with any other characteristics, we also tested for effects of 5 categorical variables: age, sex, maternity (mothers vs non-mothers), presence of pup (female with a pup attached vs others), and source location (Las Pavas vs Tolé). As our study group contained no adult males, we could only test for a possible effect of age within females, and effect of sex within juveniles. Our sample sizes were too small to generate meaningful distributions for each variable, so we estimated confidence intervals for the relationship with rank for each of the five categorical variables (age, sex,

**Table 1** To compare dominance hierarchies between species, we used data compiled from 113 different studies by Shizuka & McDonald (2015). Vampire dominance hierarchy was compared to 172 raw interaction matrices. These were 84 different species from various taxa.

Taxon	Count
Bird	51
Carnivore	13
Elephant	10
Fish	9
Invert	4
Marsupial	3
Primate	35
Reptile	5
Rodent	3
Social Insect	15
Ungulate	24

maternity, presence of pup and source location) by bootstrapping (5000 repetitions) using the R Package 'boot' (Canty & Ripley, 2017).

### 2.2.8. Interspecies comparisons

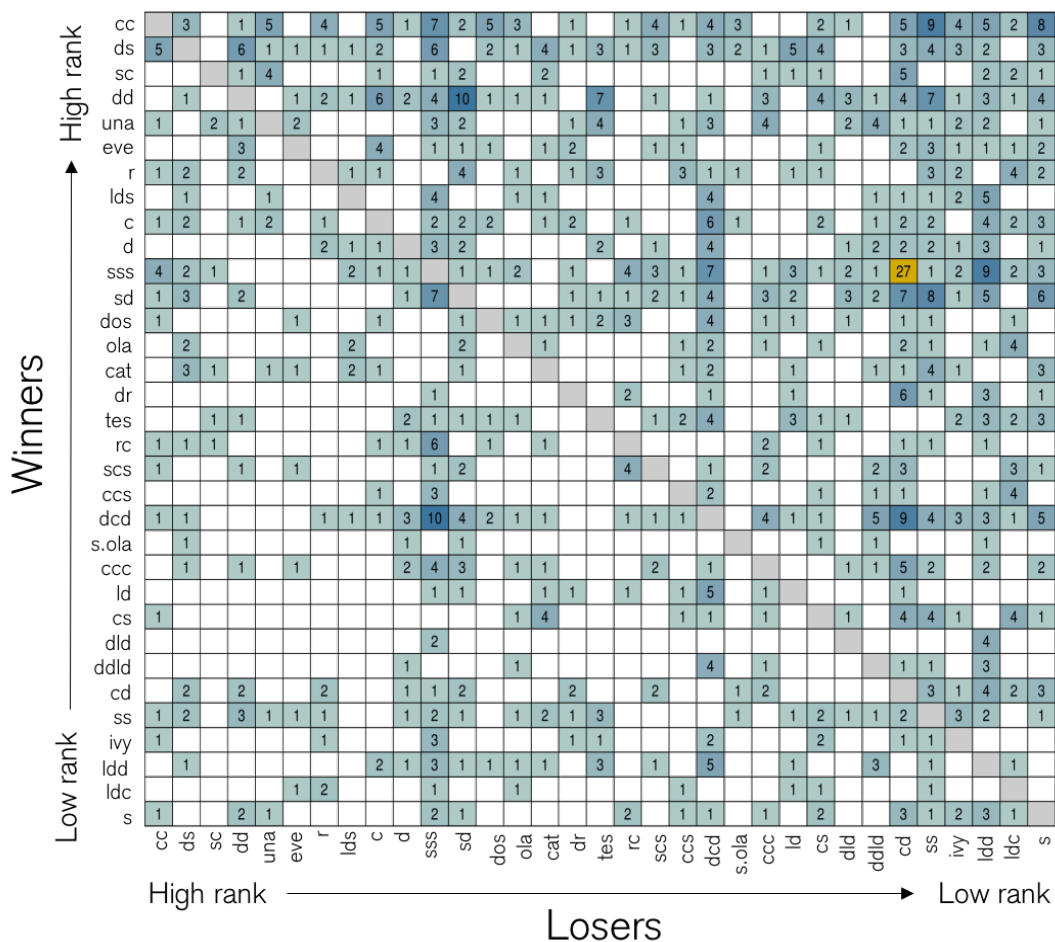
To contextualise the structure of the female vampire bat dominance hierarchy, we compared our results with other species using data compiled by Shizuka & McDonald (2015) from 113 published studies (see Table S1). These were 172 raw interaction matrices from 84 different species from various taxa including birds, mammals and invertebrates (Table 1). For

each interaction matrix, we generated network-wide measures of hierarchy structure ( $T_{tri}$ , DCI, Landau's  $h'$ ) and constructed frequency plots of those interaction matrices that were significantly ordered for each of the three metrics. For each we also calculated both measures of 'certainty' recommended by Sánchez-Tójar *et al.* (2018): 'uncertainty by repeatability' and 'uncertainty by splitting' for all 172 matrices and visually compared those to our observed values by constructing frequency distributions.

## 2.3. Results

### 2.3.1. Sampling effort

We observed 1300 win-loss interactions, 1038 of which involved winners and losers that could both be clearly identified (Figure 1). All subjects in our study (N=33 bats) were involved in at least one win-loss interaction apart from the four youngest bats because they were either not yet born, attached to their mothers during the observation period, or were too young to be tagged and identified. The number of observations per bat ranged from 15 observations (for a male juvenile “s.ola” aged 3 to 6 months) to 185 observations (for a female adult “sss”). The average number



**Figure 1** Raw interaction matrix. Outcomes of dyadic competitive interactions observed between 33 captive vampire bats ordered by randomised Elo-rating. Numbers in boxes and shading indicate the number of times a dyad were observed to interact, with darker shades indicating dyads that interacted the most. Vertical columns are number of losses while horizontal rows are number of wins. Blank boxes indicate dyads that were not observed to interact and grey boxes are self-dyads.

of interactions per individual was 31.5 (SD=6.3), which meets the 20-30 recommended for reliable results (Sánchez-Tójar *et al.*, 2018). The mean proportion of dyads observed to interact was 0.66 (SD=0.05) which exceeded the 0.47 expected by chance to interact following a Poisson distribution, suggesting a sufficient sampling effort (Sánchez-Tójar *et al.*, 2018).

### 2.3.2. Dominance interactions

We detected significant positive correlations between 8 out of 10 possible combinations of the 5 different win-loss interaction types (Table 2). We failed to find evidence that wins from ‘defence push’ predicted wins by ‘intrude push’ or ‘intrude no push’. An interaction matrix containing all displacement interactions significantly and positively correlated with a matrix containing waiting interactions. This indicates that individuals that won by any type of displacement could predict the individuals that won in ‘waiting’ interactions. Because these matrices had the highest sample

**Table 2** Pairwise Pearson’s correlation coefficients for interaction matrices separated by win-loss interaction type. Significant relationships are in bold.

			<i>r</i> -statistic	<i>p</i> -value	N
Defence no push	x	Defence Push	0.28	<b>&lt;0.01</b>	328
	x	Intrude Push	0.23	<b>&lt;0.01</b>	335
	x	Intrude no push	0.11	<b>0.02</b>	362
	x	Waiting	0.14	<b>0.01</b>	330
Defence push	x	Intrude push	0.08	0.07	443
	x	Intrude no push	0.06	0.11	470
	x	Waiting	0.21	<b>&lt;0.01</b>	438
Intrude push	x	Intrude no push	0.23	<b>&lt;0.01</b>	477
	x	Waiting	0.15	<b>&lt;0.01</b>	445
Intrude no push	x	Waiting	0.21	<b>&lt;0.01</b>	472
All displacements	x	Waiting	0.28	<b>&lt;0.01</b>	1021

size (1021) and the highest correlation coefficient ( $r$ -statistic = 0.28) we consequently used all of the interaction data we collected for the subsequent analyses.

### 2.3.3. Structure of the hierarchy

All types of competitive interactions (defend no push, defend push, intrude no push, intrude push and waiting) were similarly ordered by all three measures of structure (DCI,  $h'$  &  $T_{tri}$ ; Table 3). The similarity in orderliness values provides evidence that the observed interaction types may all be caused by the same underlying dominance structure. We had a reasonable degree of coverage because we observed a high number of possible dyads interacting: Of 528 possible dyadic relationships, 350 were observed to interact at least once by one of the 5 interaction types. No interactions were observed between 178 of the possible dyads. Of those dyads in which dominance behaviours did occur, 210 could be classified as 'unidirectional', meaning one member of dyad won more dominance interactions than the other. There was not one specific interaction type that was consistently more ordered than the rest by any of the three measures of orderliness. For instance, 'defence no push' had the strongest directionality (DCI= 0.98,  $p < 0.01$ ), but was not significantly linear by either measure of linearity ( $T_{tri} = 0.56$ ,  $p = 0.08$ ;  $h' = 0.14$ ,  $p = 0.09$ ) and occurred in fewer dyads than it did not ('defence no push' did not occur in 415 dyads out of a possible 528) indicating that it is a poor parameter of dominance behaviour alone (van Hooff & Wensing, 1987). Combining all win-loss interaction types resulted in a hierarchy that was highly linear ( $T_{tri} = 0.58$ ,  $p < 0.01$ ;  $h' = 0.27$ ,  $p < 0.01$ ), but was less directional than others (DCI=0.61,  $p = 0.01$ ). Because there was no single interaction type that was highly and significantly ordered by all three measures, and to maximise statistical power, we summed all win-loss

interaction types for all subsequent analyses. These were simply added because we had no strong *a priori* reason to give a greater weighting to any of the measures over any other.

**Table 3** Results of alternative measures of dominance hierarchy orderliness from different win-loss interaction types. Of all possible dyads within the group (528), dyads were defined as ‘unidirectional’ when one member of the dyad won more over its opponent via a particular win-loss interaction type. ‘Unknown’ denotes the number of possible dyads that were not observed to interact via a particular win-loss. Significant results are in bold.

Interaction type	N	Directional Consistency		Triangle Transitivity		Landau’s linearity		Relationships <i>Possible = 528</i>	
		DCI	<i>p</i> -value	$T_{tri}$	<i>p</i> -value	$h'$	<i>p</i> -value	Uni-directional	Unknown
Defend no push	110	0.98	<b>&lt;0.01</b>	0.56	0.08	0.14	0.09	80	415
Defend push	218	0.85	<b>&lt;0.01</b>	0.51	<b>&lt;0.01</b>	0.13	0.11	124	391
Intrude no push	252	0.82	<b>&lt;0.01</b>	0.31	<b>0.04</b>	0.11	0.21	138	360
Intrude push	225	0.75	<b>&lt;0.01</b>	0.60	<b>&lt;0.01</b>	0.12	0.14	132	377
Waiting	220	0.84	<b>&lt;0.01</b>	0.35	<b>0.03</b>	0.12	0.15	128	384
All win types	1038	0.61	<b>&lt;0.01</b>	0.58	<b>&lt;0.01</b>	0.27	<b>&lt;0.01</b>	210	178



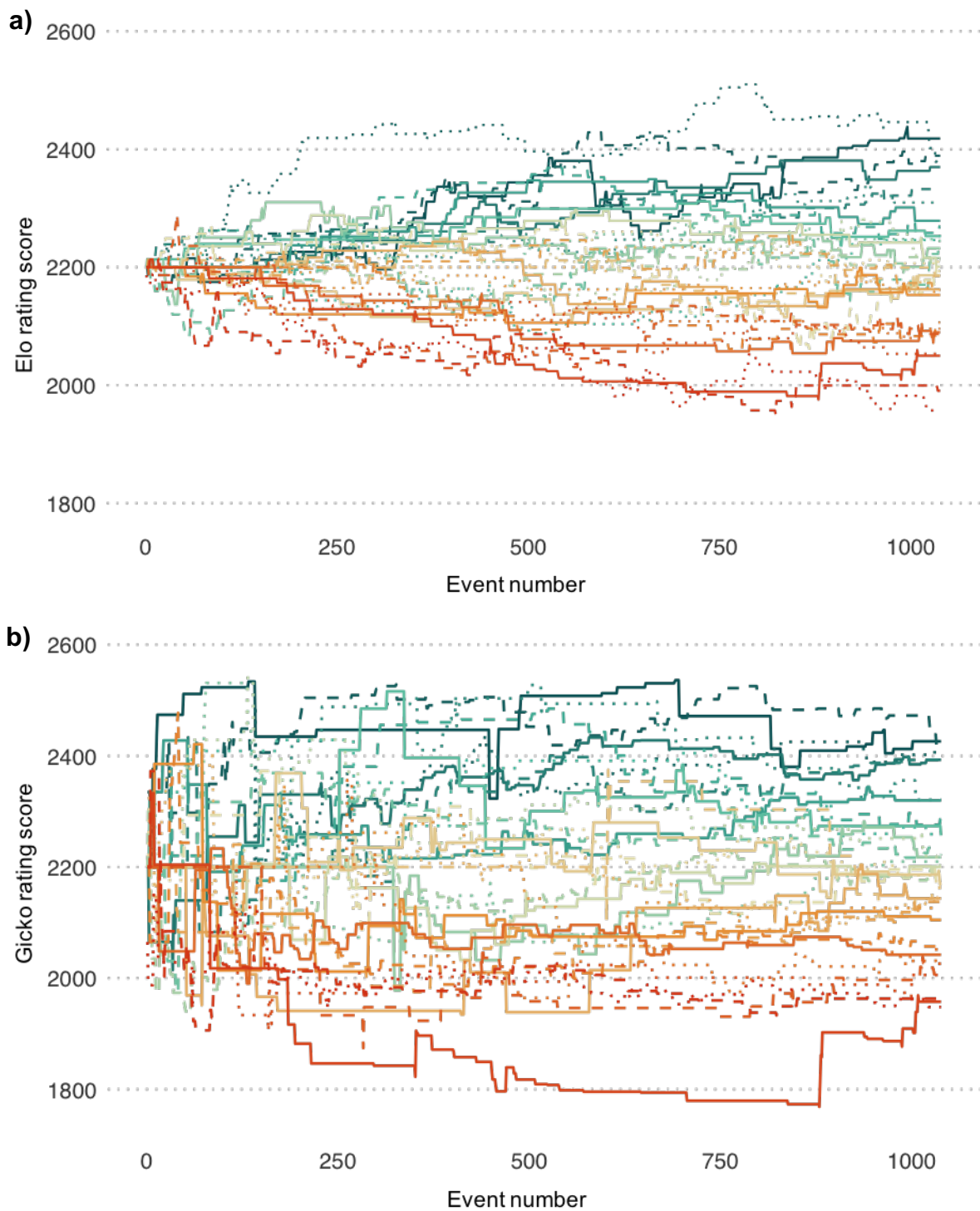
### 2.3.4. Individual ranks

All three methods used to generate individual ranks resulted in different but highly correlated rank orders (Table 4; observed individual rank orders: Table S2). Visual comparison of null and observed rank trajectory plots of both Elo-rating and Glicko-rating confirmed that there was an order to the observed interactions (Figures 2 & 3).

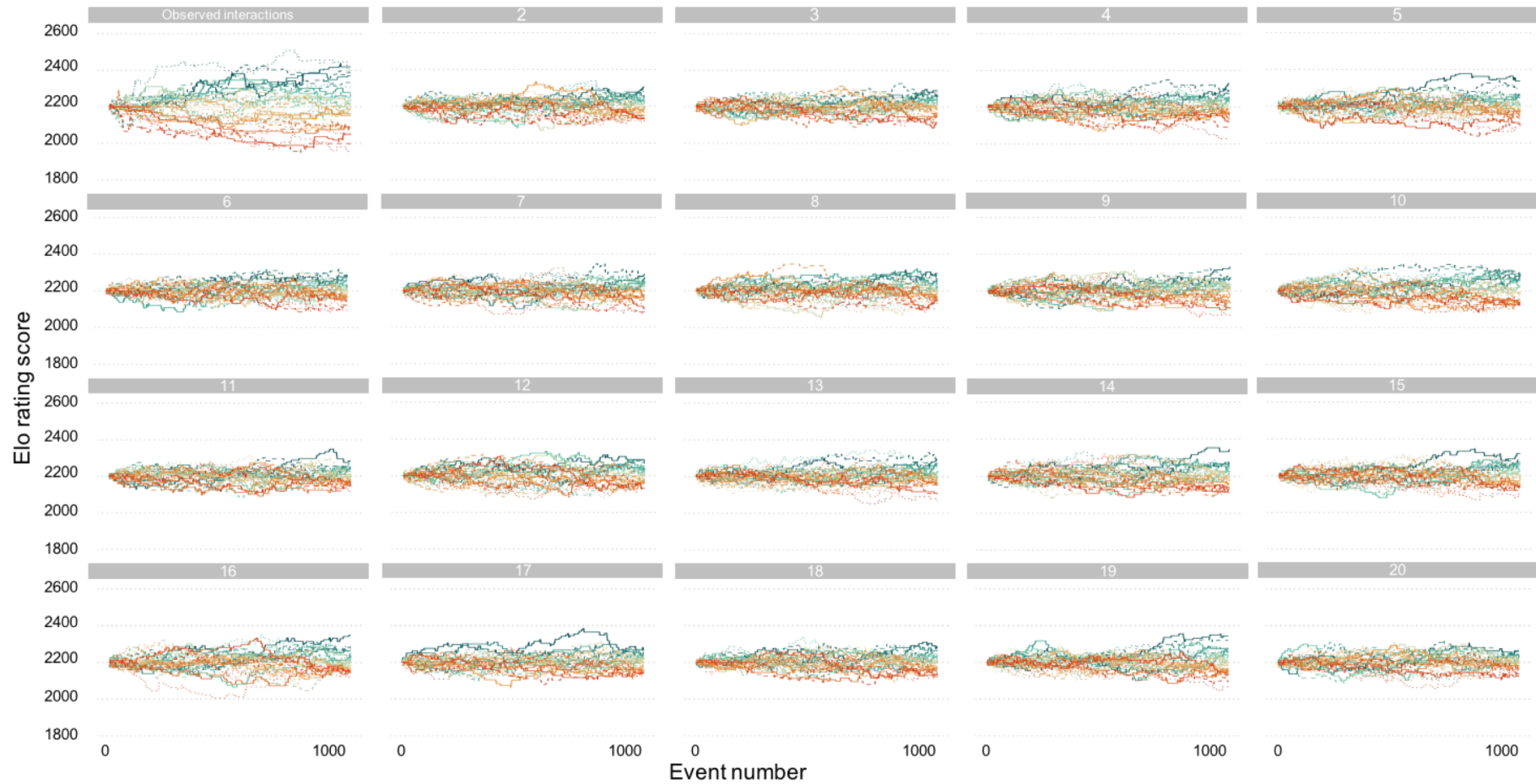
When rank was assigned using randomised Elo-rating, there was low overlap between the confidence intervals of the ranks of the highest and lowest ranking bats. Between adjacently ranked bats, however, there was a high degree of overlap in confidence intervals (Figure 5). These results indicate that while high and low ranking bats may be reliably distinguished from one another, the assigned ranks of adjacently ranked bats were not highly reliable. Likewise, there was a shallow relationship between the probability of winning and the difference in rank, meaning that the outcome of a competitive interaction was not highly predictable until there was a large difference in rank (Figure 6). Further, randomised Elo-rating ranks were not highly repeatable: We obtained a randomised Elo-rating repeatability of 0.45 and an  $r_s$  of 0.14. Taken together, these results indicate that the hierarchy was not steep.

**Table 4** Pearson’s correlation coefficients for individual rank orders obtained using three alternative methods.

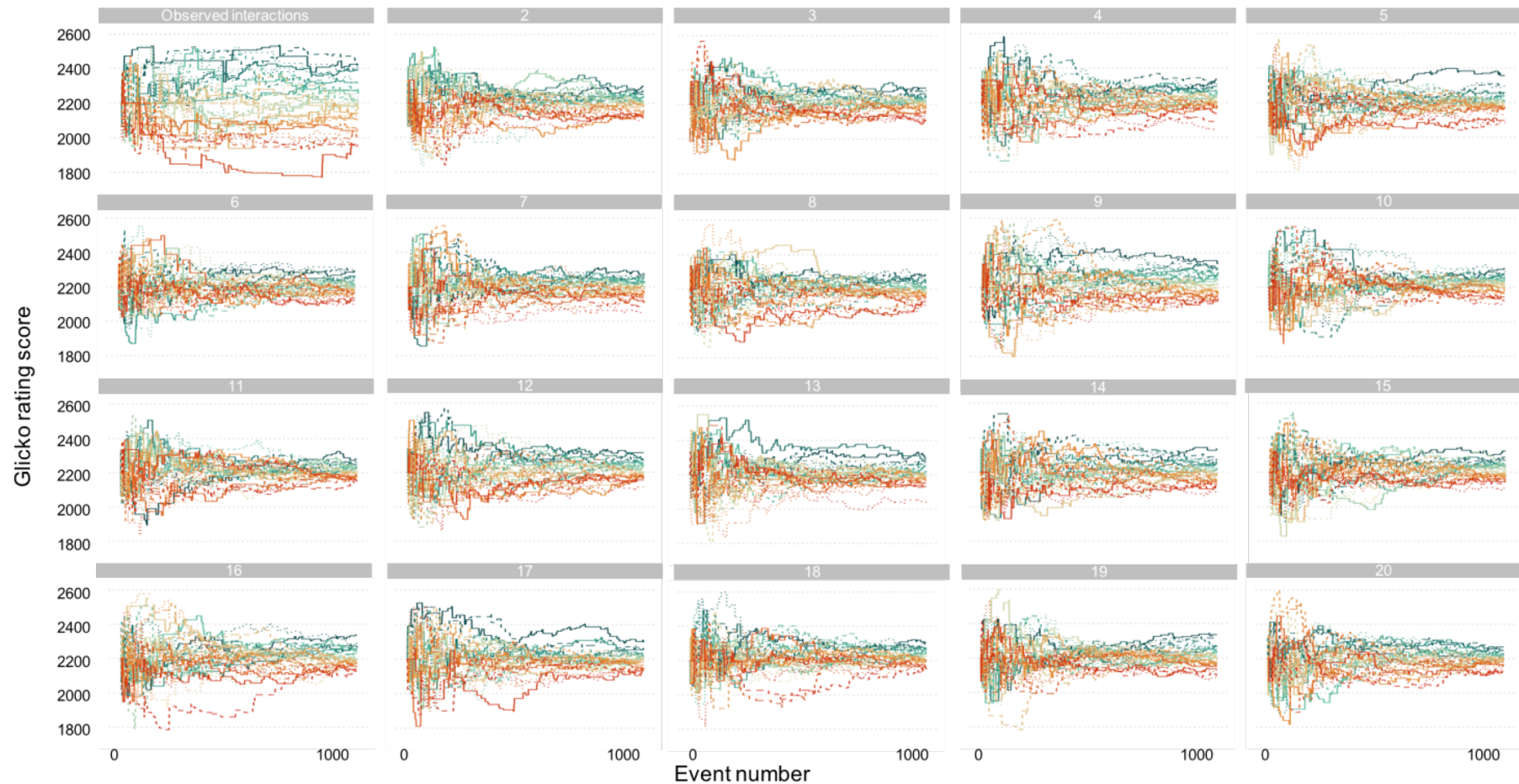
			t-statistic	DF	r-statistic	p-value
David’s rank	x	Elo rank	19.0	31	0.96	<0.01
David’s rank	x	Glicko rank	22.9	31	0.97	<0.01
Elo rank	x	Glicko rank	18.4	31	0.96	<0.01



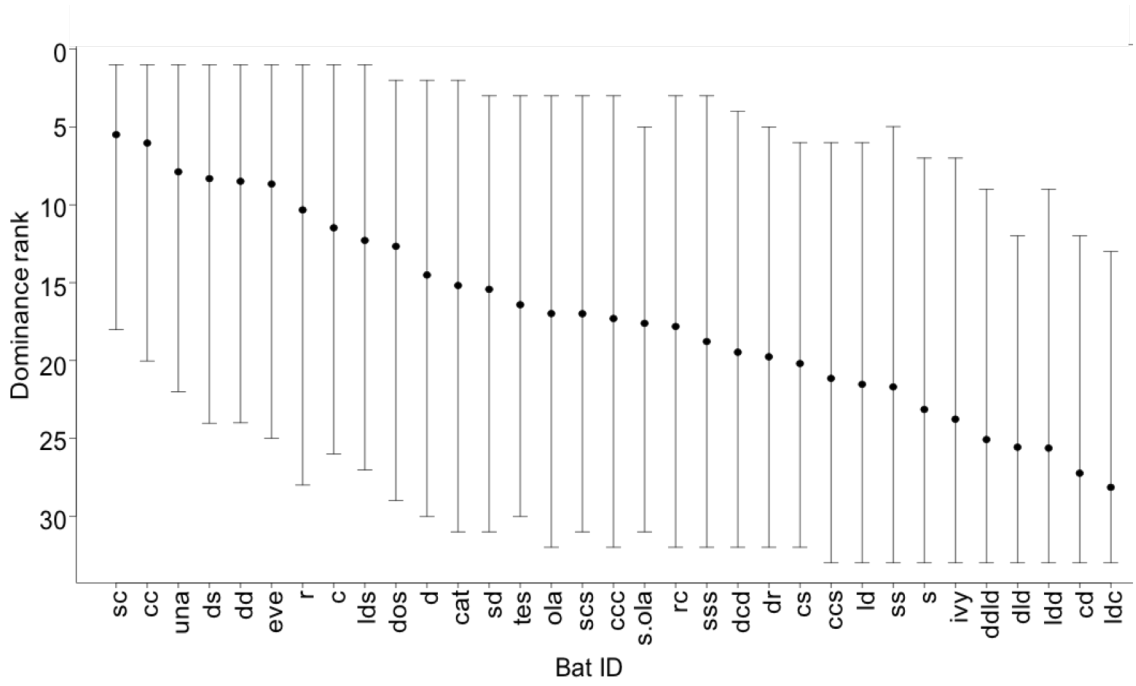
**Figure 2** Individual ranks over time calculated using a) Elo-rating and b) Glicko-rating. In both methods, each individual (coloured lines,  $N=33$ ) are assigned identical starting scores (2200). With each competitive interaction ( $y$ ), individuals gain or lose points if they win or lose, respectively. A crossover of lines indicates a rank change, in which an individual's score has changed sufficiently to change their rank relative to the other group members. Plateau of rank trajectories indicates that ranks are stable.



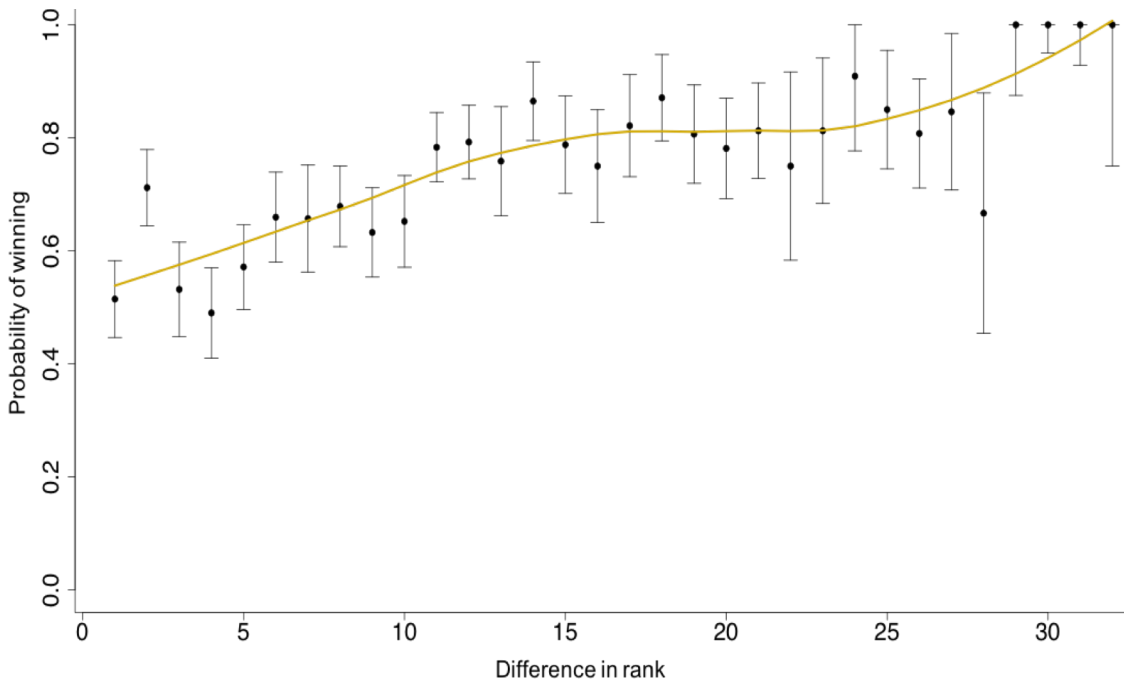
**Figure 3** Rank trajectory plots of observed versus null data (2-20) analysed using Elo-rating. Null data were generated by replacing observed winners and losers with permuted combinations of possible actors. In the observed interaction data, there were fewer rank changes over time and rank trajectories diverged into well differentiated Glicko-rating scores. By contrast, in the null data, rank changes did not decrease over time and rank trajectories appear to converge. Rank trajectory patterns of observed data are visually distinct from those of null data which provides evidence that observed competitive interactions were ordered.



**Figure 4** Rank trajectory plots of observed versus null data (2-20) analysed using Glicko-rating. Null data were generated by replacing observed winners and losers with permuted combinations of possible actors. In the observed interaction data, there were fewer rank changes over time and rank trajectories diverged into well differentiated Glicko-rating scores. By contrast, in the null data, rank changes did not decrease over time and rank trajectories appear to converge. Rank trajectory patterns of observed data are visually distinct from those of null data which provides evidence that observed competitive interactions were ordered.



**Figure 5** Mean randomised Elo-ratings with confidence intervals from 1000 replicated datasets generated by randomising the order of interactions.



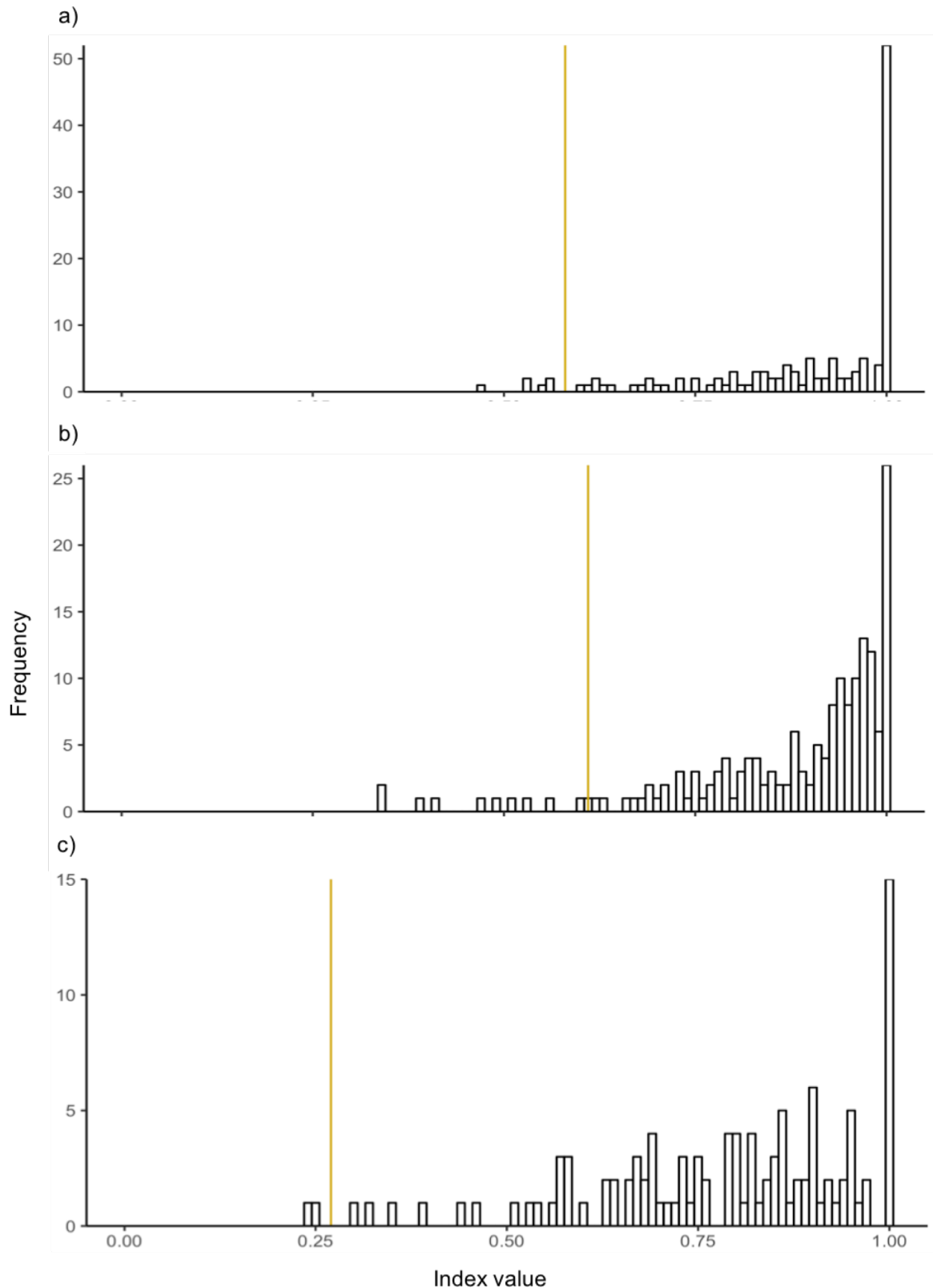
**Figure 6** Probability of a higher ranking bat winning according to difference in Elo-rank based on observed interactions. The relationship between difference in rank and probability of winning was not steep, indicating that the hierarchy was shallow.

### 2.3.5. Rank predictors

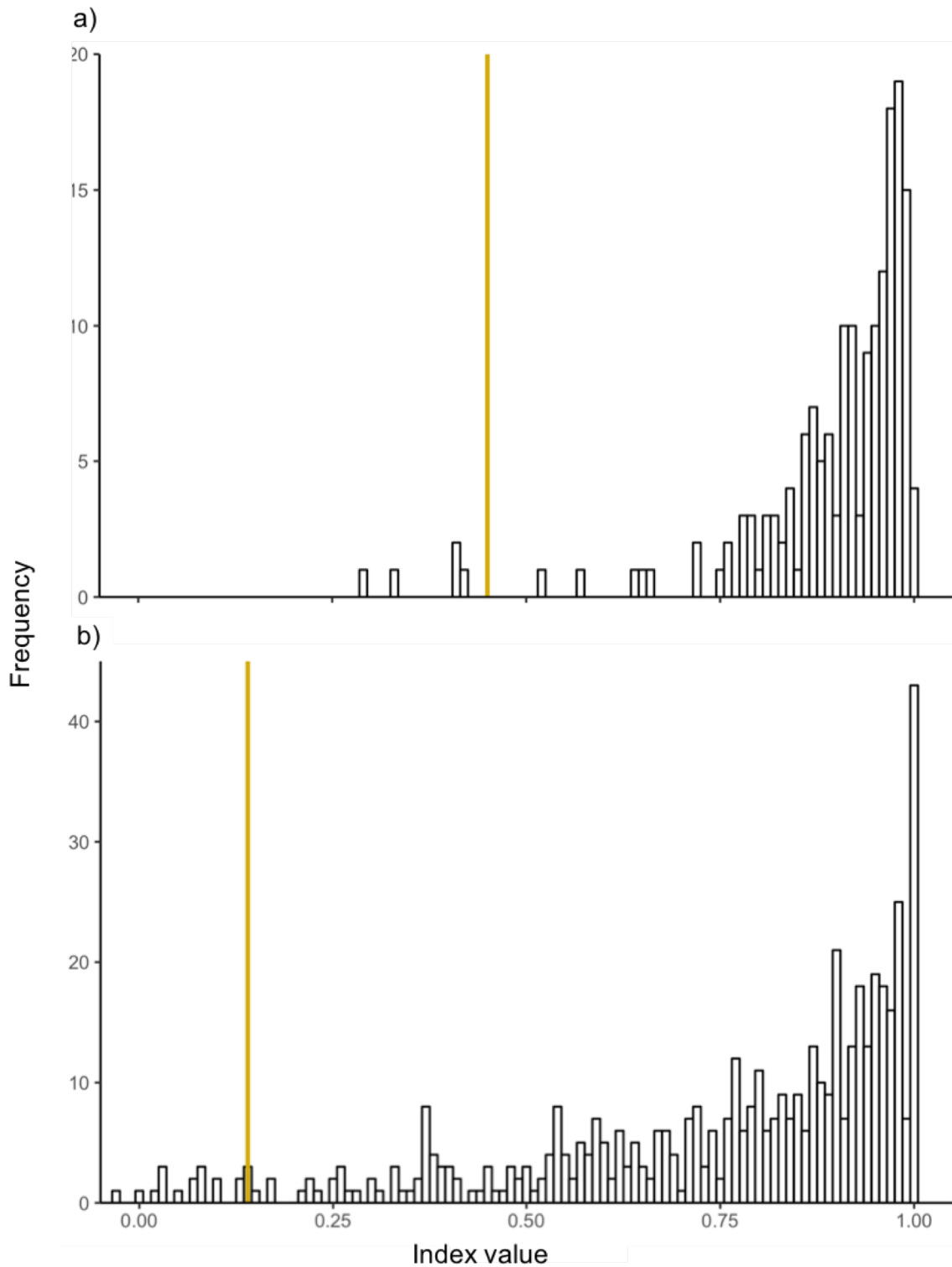
As all individual ranking methods correlated strongly with one another, analyses comparing rank to individual attributes were completed only using ranks obtained using Elo-rating. Rank was not significantly related to any predictors tested. We did not detect a relationship between rank and body mass ( $F < 0.01$ ,  $DF = 26$ , Adjusted  $R^2 = -0.04$ ,  $p = 0.96$ ), forearm length ( $F = 1.205$ ,  $DF = 27$ , Adjusted  $R^2 = 0.01$ ,  $p = 0.28$ ), female age ( $t = 1.22$ ,  $DF = 9.48$ ,  $p = 0.25$ ), or juvenile sex ( $N = 9$ ,  $t = 1.95$ ,  $DF = 5.78$ ,  $p = 0.1$ ). Among adult females, we did not detect a difference between the ranks of mothers and non-mothers ( $t = -0.31$ ,  $DF = 15.66$ ,  $p = 0.76$ ), females that had a pup attached and those that did not ( $t = -1.62$ ,  $DF = 27.13$ ,  $p = 0.12$ ), or bats caught from one site compared to the another ( $t = 0.36$ ,  $DF = 16.21$ ,  $p = 0.72$ ).

### 2.3.6. Interspecies comparisons

In comparison to other taxa, the vampire bat dominance hierarchy was weakly linear and shallow. Vampire bat females exhibit values that were in the bottom 5.5%, 4.6% and 1.8% of DCI,  $T_{tri}$  and Landau's  $h'$  values, respectively (Figure 7). Likewise, the repeatability of the vampire hierarchy was in the bottom 3% of repeatability values for the 172 other taxa, and the repeatability by splitting the hierarchy was in the bottom 5% of all values (Figure 8) indicating a comparatively low confidence in the assigned ranks and thus a relatively shallow hierarchy.



**Figure 7** Frequency distribution of significant values of three alternative measures used to characterise the overall structure of dominance hierarchies from 172 published interaction matrices from various taxa in comparison to values observed in vampire bats (yellow lines); a) DCI (N=172), b)  $T_{tri}$  (N=131) c) Landau's  $h'$  value (N=110).



**Figure 8** Certainty in assigned hierarchy estimated via two methods; a) “uncertainty by repeatability” & b) “uncertainty by splitting”. Observed value (yellow line) in comparison to that of 172 interaction matrices (bars). Indices of 1 indicate high confidence in assigned ranks.



## 2.4. Discussion

We found that female vampire bats form a weakly linear and shallow dominance hierarchy. We found strong evidence for a non-random dominance structure to competitive interactions overall and we were able to reliably distinguish high and low ranked bats. When there was a large difference in ranks, the outcome of competitive interactions was highly predictable. In contrast, the ranks of mid-ranking bats were not highly distinct from one another and we could not reliably distinguish between adjacently ranked bats. These findings, however, are consistent with weakly linear hierarchies. Previous authors have highlighted that low, albeit significant, levels of linearity may be difficult to order at the level of the individual (de Vries, 1998).

We did not find evidence that rank could be predicted by size, sex, age, reproductive status or location of origin. We may not have detected a correlation because the ranks we assigned were not precise due to the shallow nature of the hierarchy. It is also possible that rank is not determined by physical characteristics. Differences in winning ability, and thus social rank, may be determined via winner loser effects, in which previous history of winning or losing influences subsequent performance in competitive encounters (Hsu, Early & Wolfe, 2006).

The female vampire bat hierarchy might be less linear than the male dominance hierarchy. Currently there has not been a study of social rank in male vampire bats utilising methods to determine the linearity of their hierarchy. Despite this, there is good reason to believe that males form highly linear hierarchies. Roosts of females will typically be occupied by one, dominant, male who copulates the most (Wilkinson, 1985b) and actively defends the highest position in the roost, where females reside (Park, 1991), for an average of 12.8 months (Wilkinson, 1985b). All other males occupy positions lower in the roost or elsewhere (Park,

1991) and copulate less (Wilkinson, 1985b). These observations are consistent with a linear or despotic dominance hierarchy. To determine whether males form a more linear dominance hierarchy than females, it would be necessary to conduct a rigorous study using methods outlined in this study. The causes and consequences of social rank is expected to be different in males and females (Clutton-Brock & Huchard, 2013). For instance, wild eastern chimpanzee (*Pan troglodytes schweinfurthii*) males challenge conspecifics to gain rank, meanwhile females queue (Foerester *et al.*, 2016). Understanding the relative role of social rank in male and female vampire bats may be of particular interest because males, unlike females, do not form long term cooperative social bonds in the wild (DeNault & McFarlane, 1995).

Compared to other taxa, the female vampire bat hierarchy was not the least linear but fell within the lower ranges of all three metrics of linearity examined. Similarly, the vampire hierarchy was less steep and thus less repeatable/less certain than over 90% of other taxa. Female vampire bat ranks therefore appear to be either less stable over time, less linear, or less despotic than many other species studied to date.

#### 2.4.1. Possible consequences of a shallow hierarchy

The low steepness of the dominance hierarchy may have important implications for female vampire bat social behaviour. According to biological market theory (Noë & Hammerstein, 1994), cooperative investments, such as social grooming, might be exchanged for tolerance. If so, hierarchy steepness and the degree of intraspecific competition should co-vary with patterns of cooperative behaviours. Despotic hierarchies are expected to be characterised by asymmetrical cooperative behaviours because lower ranked animals should preferentially groom

higher ranked animals who can better provide rank related benefits such as coalitionary support (Henzi & Barrett, 1999; Seyfarth, 1977). Indeed, among primates, the degree of grooming directed up the hierarchy is stronger the steeper the hierarchy (Schino, 2008). Meanwhile, where there is low competition over resources in shallow, egalitarian societies, one expects more symmetrical cooperative behaviours. For instance, grooming bouts should be 'time-matched', meaning that partners should spend equal amounts of time performing and receiving grooming (Barrett *et al.*, 1999). Grooming symmetry should be weaker with rank distance and variance in grooming symmetry should vary with resource holding potential or levels of feeding competition. There is some evidence to suggest that grooming is reciprocated regardless of the steepness of the hierarchy (Kaburu & Newton Fisher, 2015; Leinfelder *et al.*, 2001) but most studies associate reciprocity with egalitarian groups (de Waal, 1986; Cheney, 1992).

Vampire bat grooming and food-sharing relationships are fairly symmetrical: The best predictor of the amount of food a bat receives from a partner is the reciprocal food and grooming given to that partner, even when controlling for kinship (Carter & Wilkinson, 2013). Taking together the role of reciprocity in vampire bat relationships with the low slope the hierarchy, our results are consistent with biological market theory of cooperative relationships. To further test support of this theory, it would be necessary to conduct a study of grooming and sharing rates in association with rank distance. Because we lacked the resolution to reliably distinguish ranks between closely ranked bats, it would not be possible to correlate cooperative behaviours at the level of the individual. We could, instead, utilize rank category, i.e. high or low rank, which we would be able to reliably assign. We would expect that the strongest relationships should occur between those of a similar rank. Those closer in rank should spend a more similar amount of time grooming and

food sharing with one another. Meanwhile, relationships that occur between individuals with a higher distance in rank should be less symmetrical in time spent grooming and food sharing.

#### 2.4.2. Possible cause of a shallow hierarchy

Socio-ecological models of non-human primate social systems predict that the steepness of female dominance hierarchies should be influenced most by intraspecific competition (Janson & van Schaik, 1988; Koenig *et al.*, 2013). High within-group competition should lead to steep, stable, nepotistic hierarchies in which there is relatively high skew in fitness outcomes and considerable benefits to the formation of coalitions. In contrast, where intraspecific competition is low (or between group competition is high), we should expect tolerant, shallow hierarchies. Where within-group competition is intermediate or food patches are not easily defensible, dominance should be individually determined by factors such as age or tenure and maintained by winner/loser effects. These 'individualistic' hierarchies are not expected to be stable, and there should be less benefit to the formation of alliances or supporting kin (Sterck, 1997; van Schaik, 1989; Wrangham, 1980).

Based on the predictions of socio-ecological models, the shallow nature of the vampire bat hierarchy could suggest that vampire bats do not experience high levels of intraspecific competition. If this is the case, our results could support two predictions of socioecological models. One, that under low intraspecific competition, hierarchies should not be steep. Two, that shallow hierarchies should be characterized by unstable ranks in which differences in competitive ability are maintained by winner/loser effects. It should, however, also be noted that the present vampire bat diet does not reflect what they experienced in their evolutionary history. Prior to the introduction of cattle and other domesticated animals to Central

America in the 16<sup>th</sup> century (Crosby, 1972), prey, which would have included large mammals such as tapir and peccary, was likely far more scarce, variable and unpredictably distributed within dense, complex habitats. If hosts were more easily monopolisable in these circumstances, it is thus possible that vampire bats formed steeper dominance hierarchies in the past if vampire bat hierarchies follow the predictions of socioecological models.

There are a number of reasons that the applicability of these socio-economical models is limited in explaining the causes and consequences of dominance hierarchies in vampire bats. Firstly, socio-ecological models predict that the formation of social bonds should be strongest where there are highly linear dominance hierarchies. This does not appear to be the case in vampire bats, since they form cooperative social bonds but do not form a highly linear dominance hierarchy. Secondly, the concept that increased intraspecific competition drives variance in hierarchy steepness may not be applicable to taxa other than primates. Some taxa, such as cooperatively hunting carnivores, aggregate in order to help each other obtain and *share* resources (Johnson *et al.*, 2002; Dalerum, 2007). In these cases, resource competition may play less of a role in structuring hierarchies. For instance, in spotted hyenas (*Crocuta crocuta*), increased within-group competition leads to group fission (Smith *et al.*, 2008), not steeper hierarchies. Social rank in cooperative carnivores may function primarily to coordinate hunting activities (see Bonanni *et al.*, 2017) rather than to order access to resources. Similar to cooperative hunting carnivores, vampire bats sociality is also associated with sharing of food. Cooperative food sharing evolved to buffer against starvation which could occur as a result of failing to locate food or feed successfully (Wilkinson, 1984; Wilkinson, 1985a; Wilkinson, 1985b). Competitively excluding colony mates from wound sites could thus be maladaptive as it could later increase cooperative food

sharing demands. To this extent, increased intraspecific competition could arguably serve to *promote* tolerance at feeding sites rather than increase defensive behaviours.

To gain an understanding of whether factors, such as food sharing, influence variation in dominance hierarchies or whether vampire bat dominance is indeed exceptional from that of other species, it would be useful to conduct a phylogenetically controlled comparative study of the structure of dominance hierarchies across taxa. Our basic comparison indicates that there is considerable variation across taxa in both hierarchy steepness and linearity. But, our analysis only informs us of the distribution of these metrics. A fully controlled phylogenetic study was beyond the extent of this study but would be necessary in order to make wider inferences about ecological or social drivers behind variation in hierarchy steepness. By controlling for phylogeny, it could also be possible to examine whether co-vary with other life history traits. For instance, it would be possible to explore the notion of whether taxa that aggregate in order to share resources, such as cooperative carnivores or vampire bats, form hierarchies that are distinctly different from those that aggregate due to other forces such as defence against predators.

#### 2.4.3. Challenges in the study of dominance hierarchies

There are a number of challenges to studying dominance hierarchies, particularly when in a species in which social rank has not previously been studied. First, measured rates of directed behaviour are often under-sampled and imprecise (Carter, Schino & Farine, 2018). In our study, the precision of the displacement rate between bat A and B is limited by the number of samples of that dyad. Although we used methods to determine that we had collected sufficient samples to estimate

rank, our study might have benefitted from additional sampling if it would have improved the resolution of our assigned ranks. Further, many dyads were sampled just once or twice, and some individuals were sampled as little as 15 times (Figure 1). The methods we used to determine our sampling effort accounted for the average rate of interaction and the mean proportion expected to interact. These methods did not account for the range of observations, which may have been an important consideration.

Second, even if the probability estimate of A “winning” against B is precise, the sampled behaviours could be a poor proxy for the actual dominance relationship. For example, subordinate individuals could in theory “displace” dominant individuals if the higher ranked bat simply find them irritating or aversive. We made efforts to establish that the behaviours we studied were good measures of dominance relationships to minimise these limitations. By correlating each win type against the others, we were able to determine that winning in one domain could predict winning in another. If interactions could be won through ways other than social dominance, we would not have expected those interaction types to correlate as highly as they did. There may, however, have been other behaviours we did not observe that could constitute dominance. For instance, vocalisations could play a role in interactions at feeders, however it is difficult to collect this type of data in bats.

Third, the rate of interaction (rather than the type of interaction) could be driven by social rank. We observed that many but not all (66%) of the possible dyads actually interacted. This could mean that (1) individuals tended to feed at non-random times or conditions, (2) there was not adequate competition to induce dominance behaviour, or (3) certain individuals actively avoided each other. The third case means that dominance interactions could have been occurring discreetly

without direct interaction (Appleby, 1983). If dominance interactions were simply rare, this could indicate that social dominance is a *weak* determinant of resource access among the captive vampire bats as per the results of this study. Alternatively, if many dyads did not interact because low ranking bats actively avoid high ranking bats, then this would suggest that dominance is a *strong* determinant of social interactions and resource access. Additional sampling can help to tease apart the source of so-called “null dyads” (de Vries *et al.*, 2006), but it is difficult to distinguish between these scenarios post-hoc (Shizuka & McDonald, 2012).

Nevertheless, it is likely that the three limitations outlined above would at most lead us to underestimate the underlying dominance structure. Our results thus indicate that there is, at the very least, a weak dominance structure to competitive interactions.

Fourth, it was necessary to study this behaviour in captivity because in order to assign social rank, we needed to be able to reliably identify bats individually. Studying behaviour in captivity introduces a number of constraints and may limit our conclusions because conditions in captivity may not resemble natural conditions and may consequently impact social behaviour. For instance, the captive bats observed in this study were able to feed *ad libitum* throughout the night and had been experiencing such a schedule for over one year prior. It could be argued that these conditions would relax the occurrence of competition and physical interaction at feeders since food in captivity was presumably more abundant and readily available than in the wild. It is possible that we observed dynamics that do not reflect those that occur in the wild.

And, finally, there are some methodological limitations in the study of dominance hierarchies. In this study, we chose to use multiple different methods. We chose this approach in order to thoroughly inspect our data but also because



currently there is no single widely-used methodology to study dominance, particularly if a species' dominance has not yet been studied. It would be greatly beneficial for a standard method of inferring dominance hierarchies to be adopted or outlined. This would also have the added benefit of allowing results to be more easily comparable.

To conclude, we found strong evidence that vampire bats form a hierarchy that is weak and shallow, particularly in comparison to other taxa. According to the biological market model of cooperative relationships, the reciprocal nature of vampire bat cooperative behaviour could be consistent with the low slope of the hierarchy. If this is the case, we may expect rank to influence the degree to which grooming and food sharing is reciprocal, but only when there is a large difference in rank. According to socioecological models of dominance hierarchies, the low slope could be a consequence of low intraspecific competition over food sources. However, given that socioecological models may be less applicable to species, such as hyenas, that aggregate in order to share food, it may also be worth considering whether the food sharing behaviour of vampire bats could influence the role that dominance plays within their social behaviour. If so, further study of social rank in relation to food sharing behaviour in vampire bats could provide greater insight into the socioecological influences of dominance hierarchies across taxa.

Moreover, it is important to note that in comparison to most other species studied, the vampire bat dominance hierarchy is exceptional for its low slope and egalitarian nature. This could illustrate one of two possibilities. Firstly, it's possible that the published datasets we used in our analysis do not represent the full range of hierarchy slopes that occur in nature. In this sense, there may be other such highly-cooperative species that have a low-sloped hierarchy comparable to that of vampire bats, but they are not well represented in the published literature.

Alternatively, it's possible that the vampire bat hierarchy is indeed extraordinarily egalitarian. Given that vampire bat cooperation is also well-studied and considered to be highly exceptional both among bats and mammals, it would be highly valuable to inspect their competitive interactions and social dominance further.

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## Supplementary Material

**Table S1** Sources of raw interaction matrices used for interspecies comparisons as compiled by Shizuka & McDonald (2015).

Source	Taxon	Species	N
Allee & Dickinson (1954)	Fish	<i>Mustelus canis</i>	10
Appleby (1983)	Ungulate	<i>Cervus elaphus</i>	7
Archie <i>et al.</i> (2006)	Elephant	<i>Loxodonta africana</i>	8
Archie <i>et al.</i> (2006)	Elephant	<i>Loxodonta africana</i>	10
Archie <i>et al.</i> (2006)	Elephant	<i>Loxodonta africana</i>	6
Archie <i>et al.</i> (2006)	Elephant	<i>Loxodonta africana</i>	6
Archie <i>et al.</i> (2006)	Elephant	<i>Loxodonta africana</i>	11
Archie <i>et al.</i> (2006)	Elephant	<i>Loxodonta africana</i>	7
Archie <i>et al.</i> (2006)	Elephant	<i>Loxodonta africana</i>	9
Archie <i>et al.</i> (2006)	Elephant	<i>Loxodonta africana</i>	9
Archie <i>et al.</i> (2006)	Elephant	<i>Loxodonta africana</i>	6
Barette & Vandal (1986)	Ungulate	<i>Rangifer tarandus</i>	20
Bennett (1939)	Bird	<i>Streptopelia risoria</i>	9
Berman, Ionica & Li (2004)	Primate	<i>Macaca thibetana</i>	22
Blatrix & Herbers (2004)	Social Insect	<i>Protomognathus americanus</i>	16
Blatrix & Herbers (2004)	Social Insect	<i>Protomognathus americanus</i>	8
Blatrix & Herbers (2004)	Social Insect	<i>Protomognathus americanus</i>	12
Blatrix & Herbers (2004)	Social Insect	<i>Protomognathus americanus</i>	6
Blatrix & Herbers (2004)	Social Insect	<i>Protomognathus americanus</i>	8
Bonanni <i>et al.</i> (2007)	Carnivore	<i>Felis catus</i>	14
Bromley (1991)	Ungulate	<i>Antilocapra americana</i>	8
Cafazzo <i>et al.</i> (2010)	Carnivore	<i>Canis lupus</i>	27

Cheney (1977)	Primate	<i>Papio cynocephalus</i>	12
Clutton-Brock <i>et al.</i> (1976)	Ungulate	<i>Equus caballus</i>	17
Collias (1950)	Ungulate	<i>Odocoileus virginianus</i>	9
Collias (1950)	Ungulate	<i>Tragelaphus angasi</i>	7
Collias & Taber (1951)	Bird	<i>Phasianus colchicus</i>	9
Collias & Taber (1951)	Bird	<i>Phasianus colchicus</i>	8
Collias & Taber (1951)	Bird	<i>Phasianus colchicus</i>	14
Cote (2000)	Ungulate	<i>Oreamnos americanus</i>	45
David & Stoffels (2003)	Fish	<i>Galaxias argenteus</i>	7
David & Stoffels (2003)	Fish	<i>Galaxias argenteus</i>	9
deWaal (1977)	Primate	<i>Macaca fascicularis</i>	14
deWaal (1977)	Primate	<i>Macaca fascicularis</i>	17
deWaal & Luttrell (1985)	Primate	<i>Macaca mulatta</i>	24
Ellard & Crowell-Davis (1989)	Ungulate	<i>Equus caballus</i>	12
Fairbanks (1994)	Ungulate	<i>Antilocapra americana</i>	12
Fairbanks (1994)	Ungulate	<i>Antilocapra americana</i>	10
Fairbanks (1994)	Ungulate	<i>Antilocapra americana</i>	11
Fairbanks (1994)	Ungulate	<i>Antilocapra americana</i>	17
Farentinos (1972)	Rodent	<i>Sciurus aberti</i>	11
Fournier & Festa-Bianchet (1995)	Ungulate	<i>Oreamnos americanus</i>	30
Frank (1986)	Carnivore	<i>Crocuta crocuta</i>	25
Hartzler (1970)	Bird	<i>Parus atricapillus</i>	7
Hass & Jenni (1991)	Ungulate	<i>Ovis canadensis</i>	18
Hausfater (1975)	Primate	<i>Papio cynocephalus</i>	16
Hausfater (1975)	Primate	<i>Papio cynocephalus</i>	21
Hausfater (1975)	Primate	<i>Papio cynocephalus</i>	17
Hausfater, Altmann & Altmann (1982)	Primate	<i>Papio cynocephalus</i>	14

Hausfater, Altmann & Altmann (1982)	Primate	<i>Papio cynocephalus</i>	20
Heitor & Vicente (2010)	Ungulate	<i>Equus caballus</i>	6
Heitor, do Mar Oom & Viente (2006)	Ungulate	<i>Equus caballus</i>	11
Hewitt, McDonald & Dugdale (2009)	Carnivore	<i>Meles meles</i>	9
Hewitt, McDonald & Dugdale (2009)	Carnivore	<i>Meles meles</i>	7
Hewitt, McDonald & Dugdale (2009)	Carnivore	<i>Meles meles</i>	14
Hirovani (1994)	Ungulate	<i>Rangifer tarandus</i>	13
Holekamp & Smale (1991)	Carnivore	<i>Crocuta crocuta</i>	13
Holekamp & Smale (1993)	Carnivore	<i>Crocuta crocuta</i>	18
Isbell & Pruett (1998)	Primate	<i>Cercopithecus aethiops</i>	9
Isbell & Pruett (1998)	Primate	<i>Erythrocebus patas</i>	17
Ito (1993)	Social Insect	<i>Pachycondyla sp.</i>	8
Ito (1993)	Social Insect	<i>Pachycondyla sp.</i>	15
Ito (1993)	Social Insect	<i>Pachycondyla sp.</i>	11
Izar, Ferreira & Sato (2006)	Primate	<i>Cebus apella</i>	17
Jenks <i>et al.</i> (1995)	Carnivore	<i>Crocuta crocuta</i>	11
Kaufmann (1974)	Marsupial	<i>Macropus parryi</i>	21
Kikkawa (1980)	Bird	<i>Zosterops lateralis</i>	10
Koenig <i>et al.</i> (2004)	Primate	<i>Trachypithecus phayrei</i>	7
Kohda (1991)	Fish	<i>Tropheus moorii</i>	31
Kolodziejczyk, Kloskowski & Krogulec (2005)	Bird	<i>Haliaeetus albicilla</i>	13
Korstjens, Sterck & Noï (2002)	Primate	<i>Colobus polykomos</i>	9
Koutnik (1981)	Ungulate	<i>Odocoileus hemionus</i>	8
Lahti, Koivula & Orell (1994)	Bird	<i>Parus montanus</i>	6
Lahti, Koivula & Orell (1994)	Bird	<i>Parus montanus</i>	8
Lee & Oliver (1979)	Primate	<i>Papio cynocephalus</i>	15
Lee & Oliver (1979)	Primate	<i>Papio cynocephalus</i>	8

Lott (1979)	Ungulate	<i>Bison bison</i>	26
Lott & Galland (1987)	Ungulate	<i>Bison bison</i>	11
Lu, Koenig & Borries (2008)	Primate	<i>Semnopithecus entellus</i>	13
Marler (1955)	Bird	<i>Fringilla coelebs</i>	8
Masure & Allee (1934)	Bird	<i>Columba livia</i>	7
Mather (1985)	Invert	<i>Eledone moschata</i>	6
McMahan 1984	Primate	<i>Papio cynocephalus</i>	10
Møller (1987)	Bird	<i>Passer domesticus</i>	13
Møller (1987)	Bird	<i>Passer domesticus</i>	10
Møller (1987)	Bird	<i>Passer domesticus</i>	14
Monnin & Peeters (1999)	Social Insect	<i>Dinoponera quadriceps</i>	6
Murray (2007)	Primate	<i>Pan troglodytes</i>	18
Myrberg (1972)	Fish	<i>Eupomacentrus partitus</i>	8
Myrberg & Gruber (1974)	Fish	<i>Sphyrna tiburo</i>	10
Nakano (1994)	Fish	<i>Oncorhynchus masou</i>	11
Nakano (1995)	Fish	<i>Salvelinus leucomaenis</i>	14
Natoli & de Vito (1991)	Carnivore	<i>Felis catus</i>	14
Nelissen (1985)	Fish	<i>Melanochromis auratus</i>	7
O'shea (1976)	Rodent	<i>Xerus rutilus</i>	10
Ortius & Heinz (1995)	Social Insect	<i>Leptothorax sp.</i>	6
Owens & Owens (1996)	Carnivore	<i>Hyaena brunnea</i>	7
Paoli, Palagi & Borgognini (2006)	Primate	<i>Pan paniscus</i>	8
Parsons & Baptista (1980)	Bird	<i>Zonotrichia leucophrys</i>	8
Patterson (1977)	Bird	<i>Tadorna tadorna</i>	28
Payne, Lawes & Henzi (2003)	Primate	<i>Cercopithecus mitis</i>	9
Poisbleau <i>et al.</i> (2005)	Bird	<i>Anas acuta</i>	6
Poisbleau <i>et al.</i> (2005)	Bird	<i>Anas penelope</i>	7



Poisbleau <i>et al.</i> (2005)	Bird	<i>Anas platyrhynchos</i>	8
Poisbleau <i>et al.</i> (2006)	Bird	<i>Anas platyrhynchos</i>	16
Poisbleau <i>et al.</i> (2006)	Bird	<i>Branta bernicla</i>	19
Post (1992)	Bird	<i>Quiscalus major</i>	15
Prieto & Ryan (1978)	Reptile	<i>Sauromalus obesus</i>	18
Reason & Laird (1988)	Ungulate	<i>Addax nasomaculatus</i>	18
Richter <i>et al.</i> (2009)	Primate	<i>Macaca arctoides</i>	9
Robbins (2008)	Primate	<i>Gorilla beringei</i>	8
Röell (1978)	Bird	<i>Corvus monedula</i>	18
Rovero, Lebboroni & Chelazzi (1999)	Reptile	<i>Emys orbicularis</i>	8
Rovero, Lebboroni & Chelazzi (1999)	Reptile	<i>Emys orbicularis</i>	12
Russell (1970)	Marsupial	<i>Megaleia rufa</i>	11
Russell (1970)	Marsupial	<i>Megaleia rufa</i>	13
Rutberg (1986)	Ungulate	<i>Bison bison</i>	29
Samuels, Silk & Atlmann (1987)	Primate	<i>Papio cynocephalus</i>	19
Satoh & Ohkawara (2008)	Social Insect	<i>Vollenhovia nipponica</i>	8
Satoh & Ohkawara (2008)	Social Insect	<i>Vollenhovia nipponica</i>	9
Satoh & Ohkawara (2008)	Social Insect	<i>Vollenhovia nipponica</i>	10
Scott & Lockard (1999)	Primate	<i>Gorilla gorilla</i>	6
Scott & Lockard (1999)	Primate	<i>Gorilla gorilla</i>	6
Seibert & Crowell-Davis (2001)	Bird	<i>Nymphicus hollandicus</i>	12
Setchell & Wickings (2005)	Primate	<i>Mandrillus sphinx</i>	11
Setchell & Wickings (2005)	Primate	<i>Mandrillus sphinx</i>	8
Shoemaker (1939)	Bird	<i>Serinus canarius</i>	10
Slotow, Alcock & Rothstein (1993)	Bird	<i>Zonotrichia leucophrys</i>	10
Smith (1976)	Bird	<i>Parus atricapillus</i>	7
Solberg & Ringsby (1997)	Bird	<i>Passer domesticus</i>	9

Solberg & Ringsby (1997)	Bird	<i>Passer domesticus</i>	9
Solberg & Ringsby (1997)	Bird	<i>Passer domesticus</i>	9
Somers & Nel (1998)	Invert	<i>Potamonautes perlatus</i>	6
Somers & Nel (1998)	Invert	<i>Potamonautes perlatus</i>	8
Somers & Nel (1998)	Invert	<i>Potamonautes perlatus</i>	9
Stamps <i>et al.</i> (1978)	Reptile	<i>Anolis aeneus</i>	6
Sterck & Steenbeek (1997)	Primate	<i>Macaca fascicularis</i>	9
Struhsaker (1967)	Primate	<i>Cercopithecus aethiops</i>	12
Struhsaker (1967)	Primate	<i>Cercopithecus aethiops</i>	12
Sullivan1982	Carnivore	<i>Phoca vitulina</i>	18
Tamm (1977)	Bird	<i>Corvus monedula</i>	10
Tamura, Hayashi & Miyashita (1988)	Rodent	<i>Callosciurus erythraeus</i>	15
Tarvin & Woolfenden (1997)	Bird	<i>Cyanocitta cristata</i>	16
Thompson (1960)	Bird	<i>Carpodacus mexicanus</i>	8
Thompson (1960)	Bird	<i>Carpodacus mexicanus</i>	8
Thompson (1960)	Bird	<i>Carpodacus mexicanus</i>	8
Thompson (1960)	Bird	<i>Carpodacus mexicanus</i>	9
Thompson (1960)	Bird	<i>Carpodacus mexicanus</i>	8
Tilson & Hamilton (1984)	Carnivore	<i>Crocuta crocuta</i>	8
Torr & Shine (1996)	Reptile	<i>Lampropholis guichenoti</i>	9
Trunzer, Heinz & Holldobler (1999)	Social Insect	<i>Pachcondyla villosa</i>	19
Varley & Symmes (1966)	Primate	<i>Macaca mulatta</i>	6
Vervaecke, de Vries & van Elsacker (2000)	Primate	<i>Pan paniscus</i>	6
Watt (1986)	Bird	<i>Zonotrichia querula</i>	10
Watt (1986)	Bird	<i>Zonotrichia querula</i>	10
Watt (1986)	Bird	<i>Zonotrichia querula</i>	10
Watt (1986)	Bird	<i>Zonotrichia querula</i>	10

Watt (1986)	Bird	<i>Zonotrichia querula</i>	10
Wells & von Goldschidt-Rothschild (1979)	Ungulate	<i>Equus caballus</i>	25
West-Eberhard (1986)	Social Insect	<i>Polistes canadensis</i>	7
Williams, Kikkawa & Morris (1972)	Bird	<i>Zosterops lateralis</i>	10
Wittemeyer & Getz (2007)	Elephant	<i>Loxodonta africana</i>	20
Wittig & Boesch (2003)	Primate	<i>Pan troglodytes</i>	15
Yasukawa & Bick (1983)	Bird	<i>Junco hyemalis</i>	6
Yasukawa & Bick (1983)	Bird	<i>Junco hyemalis</i>	6
Yasukawa & Bick (1983)	Bird	<i>Junco hyemalis</i>	6
Yasukawa & Bick (1983)	Bird	<i>Junco hyemalis</i>	6
Yasukawa & Bick (1983)	Bird	<i>Junco hyemalis</i>	6
Yasukawa & Bick (1983)	Bird	<i>Junco hyemalis</i>	6
Yasukawa & Bick (1983)	Bird	<i>Junco hyemalis</i>	6
Yasukawa & Bick (1983)	Bird	<i>Junco hyemalis</i>	6
Zine & Krausman (2000)	Ungulate	<i>Ovis canadensis</i>	12

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**Table S2** Individual rank orders obtained from each of three alternative measures. Each ranking measure yielded different rank orders, yet were all highly correlated with one another.

	Rank	Davids Score	Glicko-rating	Elo-rating
<b>High rank</b>	1	cc	cc	ds
	2	dd	sc	dd
	3	ds	una	cc
	4	una	dd	una
	5	sc	ds	sc
	6	c	eve	c
	7	eve	c	eve
	8	r	r	r
	9	lds	lds	tes
	10	d	dos	lds
	11	dos	sd	sss
	12	sd	d	dos
	13	tes	cat	sd
	14	rc	scs	scs
	15	ccc	tes	cat
	16	cat	sss	d
	17	ola	ccc	dcd
<b>Low rank</b>	18	s.ola	ola	ola
	19	scs	rc	cs
	20	dr	s.ola	rc
	21	dcd	dcd	s.ola
	22	sss	ld	dr
	23	ccs	dr	ccc
	24	cs	cs	ccs
	25	ld	ccs	ld
	26	dld	ss	ivy
	27	ddld	s	dld
	28	ivy	ivy	ddld
	29	s	ddld	ss
	30	ss	dld	s
	31	ldc	ldd	ldc
	32	ldd	cd	ldd
	33	cd	ldc	cd