

Dominance among female white-faced capuchin monkeys (*Cebus capucinus*): hierarchical linearity, nepotism, strength and stability

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Summary

Research on Old World primates provided the foundation for understanding competitive strategies resulting from social and ecological pressures. The neotropical primate, *Cebus capucinus* shares many social patterns with Old World cercopithecines (e.g., female philopatry, male dispersal), which may contribute to similar expression of competitive strategies. To clarify the nature of dominance patterns among female white-faced capuchins we examined hierarchical linearity, rank acquisition, matrilineal rank inheritance, hierarchical strength and stability. We collected focal data on 22 adult females (2008) and long-term dominance data (1986–2008) on 33 adult females in Sector Santa Rosa, Costa Rica. Females displayed linear hierarchies based on the direction of dyadic submission. At sexual maturity females quickly acquired rank positions beneath their mother and older sisters. Hierarchies were considered strong based on high proportions of food-related agonism, short latency to detection of hierarchies (21 h/female) and low directional inconsistency scores (<5%). Hierarchies were considered stable based on lack of tied submissive interactions (indicative of uncontested rank positions), low rates of rank change (0.510 changes/year), and long-term stability in matrilineal rank order. These findings enhance our understanding of capuchin social systems and how the competitive strategies of white-faced capuchins compare to those of Old World primates.

Keywords: competitive strategies, rank inheritance, females, neotropical primates, social behaviour.

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Introduction

Dominance is a fundamental aspect of social organization for many gregarious mammalian species. It is defined by Drews (1993) 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. The status of the consistent winner is dominant and that of the loser is subordinate”. Thus, dominance relationships form through repeated social interactions, stabilizing in such a way that individuals can often predict the outcome of a contest situation based on previous experiences and proximate social and physical cues (Rowell, 1974; Hinde, 1976; Roney & Maestriperi, 2003). Some species rely heavily on physical differences as measures of fighting ability (e.g., size, males vs. females in sexually dimorphic species; weaponry, pushing matches by male red deer, *Cervus elaphus*: Clutton-Brock et al., 1986) to settle contests and reinforce previously established dominance relationships. Yet dominance interactions often involve the deference of one individual to the other using less physical aggressive and submissive behavioural displays such as supplantations and avoids (e.g., yellow baboons, *Papio cynocephalus*: Samuels et al., 1987; African elephants, *Loxodonta africana*: Archie et al., 2006). Contests resulting in physical injury to one or both participants are very costly so it is in the individual’s best interest to assess physical and behavioural cues to determine the resource holding power (i.e., likelihood of winning) of their opponent prior to engaging in a competitive interaction (Maynard Smith & Price, 1973). The formation of a dominance hierarchy based on repeated interactions with consistent outcomes involving behavioural cues allows the majority of contest situations to be settled without escalation and physical harm to one or more participating individuals (Kaufmann, 1983).

Many species of primate provide good models for the study of dominance as they maintain structured social groups outside of the mating season and form extensive social networks. Competitive strategies for female primates are directly tied to food resources, and resource acquisition may be enhanced by the presence of related females who behave cooperatively (Trivers, 1972; Wrangham, 1980). As a consequence of group living, female primates are faced with the dilemma of needing to cooperatively unite against predators

and other groups in competition for resources, while simultaneously competing over resources within their social group (Wrangham, 1980). According to socio-ecological models (Wrangham, 1980; van Schaik, 1989; Isbell, 1991, 2004; Sterck et al., 1997; Koenig, 2002), female dominance relationships are shaped by this 'compete versus cooperate' dilemma. Four categories (resident-nepotistic, resident-nepotistic-tolerant, resident-egalitarian and dispersal-egalitarian) describe the social responses that arise among female primates from different combinations of intra and intergroup competitive pressures (Sterck et al., 1997). Although broad categorizations of competitive regimes into these four classes may capture some of the variation seen in primate social systems, dominance relationships can also differ at the group, species, and population levels according to variation in localized (i.e., group-level) genetic, ecological and social factors, which makes modeling and 'grand schemes' difficult. Expansion of the number and scope of studies investigating dominance behaviour may reveal additional variation that will help to improve classification, cross-species comparisons and future modelling efforts.

Traditional measures of dominance such as rank acquisition and nepotistic ranking patterns provide an important indication of the type of competitive regime influencing a species. Decades of research on dominance in 'resident-nepotistic' cercopithecine species (e.g., macaques and baboons) has revealed a number of additional components of dominance among female philopatric species. Linearity, strength and stability are characteristics of hierarchies that are essential for understanding variation in dominance relationships, social structure and fitness among social primates, as is dominance style. *Cebus* are one of two platyrrhine taxa (the other being *Saimiri*) that share similar social structure and behavioural patterns with cercopithecines. However, some differences from Old World monkeys (OWM) in factors such as group size and occasional female transfer make capuchins an interesting genus with which to compare our knowledge of competitive strategies and socio-ecology among Old World primates. In this paper, we briefly describe six key components of dominance, present our project and predictions for five of them, and discuss our findings concerning the structure and characteristics of dominance hierarchies among female white-faced capuchins in Sector Santa Rosa, Costa Rica.

Components of dominance

Hierarchical linearity

Conventional methods used to construct dominance hierarchies have focused on building a rank order with assumed transitivity. However, 'perfect' linearity within the hierarchy is uncommon and organization into a linear order ignores rank reversals, which may be important in understanding social dynamics at the group, population and species level (de Vries, 1995). Furthermore, linearity may be less than perfect due to lack of expression of dominance within some dyads caused by large group size or lack of overlap in social networks, resulting in partial hierarchies (Izar et al., 2006). Although dominance hierarchies are often described as 'linear', quantification of this measure is needed both to describe the extent to which an assigned rank order reflects a species' behavioural interactions and to make comparisons within and across species.

Rank acquisition and stabilization

Hierarchies where individuals directly or indirectly gain fitness benefits from associations with kin (both in terms of acquiring rank and desired resources) are considered 'nepotistic' (Chapais & Berman, 2004). Rank acquisition and dominance relationships are often greatly influenced by matrilineal descent in Old World monkey species where offspring inherit their mother's rank (e.g., macaques and baboons). Cooperative nepotistic support subsequently leads to a consistent long-term reinforcement of rank. Rank reinforcement and stability may be adaptively important for species that rely upon clumped, high-quality resources for which access can vary according to rank and competitive ability. Holding a stable high rank position provides proximate increases in resource acquisition followed by increased health and fitness benefits and possibly higher ultimate lifetime reproductive success (e.g., long-tailed macaques, *Macaca fascicularis*: van Noordwijk & van Schaik, 1999).

Nepotism and matrilineal rank inheritance

Kawamura (1958) proposed the following principles governing matrilineal rank inheritance among a population of adult female Japanese macaques (*Macaca fuscata*): (1) daughters rank adjacent to maternal kin, (2) younger

sisters rank above older sisters and (3) mothers rank above daughters. Some other Old World monkey species follow these general principles (e.g., rhesus macaques, *Macaca mulatta*: Sade, 1967 and yellow baboons, Hausfater et al., 1982). However, subsequent research has revealed that captive environments and provisioning may create more intense resource competition that fosters a greater amount of support by mothers toward daughters in competitive situations. Thus, Kawamura's principle of youngest ascendancy may not hold in wild or un-provisioned primate populations (Furuichi, 1983; Hill & Okayasu, 1995); unrelated or more distantly related individuals may play a larger social role in such societies because life expectancy is shorter and the availability of closely related social partners is more erratic. Expanding investigation of the influence of nepotism on rank order patterning may help to elucidate the social and ecological pressures shaping dominance behaviour.

Hierarchical strength

There are key quantifiable measures that indicate hierarchical strength (i.e., how clearly a hierarchy is enforced or reflected) (Isbell & Young, 2002). First, the context of agonism is important. Groups are expected to form clear dominance hierarchies when there is direct competition that results in a differential ability to capitalize on clumped, high-quality, and usurpable resources. Groups typically lack decided dominance hierarchies or infrequently assert their dominance rank (and live in 'egalitarian societies') if they compete only indirectly for ubiquitous resources (Sterck et al., 1997). If a great proportion of interactions involving aggression and/or submission take place within the context of feeding (versus social situations), the hierarchy is typically well defined and strong (Isbell & Young, 2002).

Second, the rate of dominance expression, measured as the 'latency to detection' (i.e., the amount of time it takes to record the number of dominance interactions necessary to accurately place individuals into a hierarchy), has been found to vary among species (Isbell & Young, 2002). A high rate of submission is associated with a short 'latency to detection' and indicates a strong hierarchy. The percentage of reversals within a matrix, also referred to as the 'directional inconsistency index' (DII), is noted as a third measure of hierarchical strength (Isbell & Young, 2002). Submissive interactions that occur below the diagonal within a constructed dominance matrix are termed dominance 'reversals' since they represent agonism against the rank order. Strong hierarchies will exhibit low directional inconsistency index scores (<5%).

The amount of directional inconsistency or 'reversals' has been used in many studies and is very useful for cross-species comparisons of dominance expression (e.g., yellow baboons, Hausfater et al., 1982; vervets, *Chlorocebus aethiops*, and patas, *Erythrocebus patas*: Isbell & Pruett, 1998).

Hierarchical stability

Stability is an important descriptor of dominance hierarchies (Isbell & Young, 2002). We looked at stability with respect to individual as well as matrilineal rank. Primate species classified as 'resident-nepotistic' tend to have stable hierarchies (e.g., yellow baboons, Hausfater et al., 1982; Japanese macaques, Chapais et al., 1991). On the other hand, individualistic hierarchies often occur in species where resources are more ubiquitous and may only show moderate strength and stability (e.g., mountain gorillas, *Gorilla beringei beringei*, Robbins et al., 2005). A number of quantifiable measures have been presented to help indicate stability within a hierarchy. For example, 'high-value ties' were described by Izar et al. (2006) as dyads that have at or near 50% of dominance interactions occurring in both directions. The absence of such high-value ties is evidence for stability of dyadic relationships within a group since a bidirectional relationship would be indicative of unstable or contested rank. Furthermore, fluctuation of female group membership (i.e., female immigration, emigration, death/disappearance, or with the maturation of young adult females (5 years old) to full adult status (6 years old)) can directly influence the stability of rank positions (Chapais, 1985). Finally, the rate of rank change over time is an important descriptor of hierarchical stability that helps clarify variation in dominance behaviour among primate populations.

Dominance style

Dominance style is the level of tolerance displayed by dominant individuals toward more subordinate ones, and varies on a continuum from despotic to relaxed relationships (de Waal, 1989). Whether individuals exhibit despotic or relaxed dominance relationships depends upon the types of competitive pressures faced by a group; relationships among individuals are expected to be more tolerant when cohesive group efforts are needed to defend resources against other groups. A suite of traits including bidirectionality of aggression, level of kin bias, and conciliatory behaviour have been found to covary

among macaque species creating the range of observed dominance styles within the genus *Macaca* that has been subsequently applied to observed behaviour in other primate genera (*Macaca*: Thierry, 2000; *Colobus*: Grunau & Kuester, 2001; *Pan*: Foster et al., 2009). Although dominance style is a very important component of dominance behaviour, the topic is beyond the scope of this paper and so we address it separately (Bergstrom, 2009; Bergstrom & Fedigan, data not shown).

Study species

White-faced capuchins (*Cebus capucinus*) are gregarious New World monkeys (Platyrrhini) and belong to the family Cebidae. Their distribution ranges from northern Honduras to northern Ecuador (Fragaszy et al., 2004). The mating system is polygynandrous and groups are composed of multiple males and females with an average adult sex ratio (male/female) of 0.72 (Fedigan & Jack, 2001). Average group size ranges between 12 and 27 individuals (Fragaszy et al., 2004). Females are philopatric (Fedigan, 1993) and males typically disperse at a mean age of 4.5 years (Jack & Fedigan, 2004).

Capuchins often live in seasonal habitats (i.e., distinct rainy and dry seasons) where temporal variation in resource quality, abundance, and distribution may impact the level of competition and type of dominance relationships, kin support and rank patterning among females (Vogel et al., 2007). As highly frugivorous primates, capuchins are known to directly compete over fruit (Vogel, 2005), a high-quality, clumped and monopolizable food resource (Isbell, 1991). Nonetheless, the intense, localized competition over food resources created in provisioned environments likely fosters unusually strong kin support by mothers toward youngest daughters, creating a consistent pattern of maternal rank inheritance (e.g., Japanese macaques: Kawamura, 1958). In contrast, in a wild setting, the opportunities are greater to exploit a more extensive array of food items on a larger spatial scale. Furthermore, decreased survivorship and reproductive output in wild versus captive settings may limit the availability of close kin to foster the phenomenon of fully nepotistic rank relations. Therefore, we do not know if the competitive interactions among related female capuchins at Santa Rosa will be as intense or frequent as those previously observed in macaques that promote consistent maternal rank inheritance patterning.

Female *C. capucinus* are classified as female-bonded due to their expression of high levels of association, including strong coalitionary behaviour and nepotistic tendencies between females, as compared to other age–sex class dyads (Perry, 1996). Clear aggressive and submissive behaviours that are commonly used to determine dominance hierarchies are exhibited, even though formal submission (i.e., a consistently expressed fear behaviour that is spontaneous rather than in response to received aggression; e.g., silent bared teeth display) is not as prevalent as it is among Old World monkeys (e.g., baboons and macaques). Individuals often solicit help from social partners to form coalitions when aggressing another individual (Manson et al., 1999; Perry et al., 2004) and this triadic behaviour renders detection of dominance relationships among lower ranking individuals difficult (Fragaszy et al., 2004). Past studies have ranked individuals in a linear order within groups of white-faced capuchins (Fedigan, 1993; Perry, 1996; Manson et al., 1999), and research on other well studied capuchin species (*Cebus albifrons*, *C. apella* and *C. olivaceus*) has documented linear rank order (reviewed in Fragaszy et al., 2004). However, the degree of linearity is unknown and the strength of hierarchy remains unexplored in *Cebus* species.

O'Brien & Robinson (1993) documented a consistent rank order in wedge-capped capuchin monkeys (*Cebus olivaceus*) over a 10-year study, which provides evidence supporting hierarchical stability and strength in capuchins. Prior data on stability (in terms of rank change) for white-faced capuchins shows cross-site variation and is inconclusive, although longitudinal analysis of hierarchies shows long periods of stability interspersed with short periods of instability (Manson et al., 1999). More research is needed to clarify whether this variation is due to methodological differences between studies, limitations of the data or true differences in behaviour across groups and/or populations.

Despite the large body of information that has been acquired over the past 25 years regarding social patterns in capuchins, there is still much to be learned about dominance relationships in this genus. Information produced by this study may enhance our understanding of capuchin social systems and competitive patterns as well as help us to document how the competitive strategies of white-faced capuchins compare to those of more extensively studied Old World monkeys.

Research questions

We collected and analyzed behavioural data to investigate the following research questions based on previous research and on social patterns predicted by socio-ecological models:

- (1) Hierarchical linearity: Can white-faced capuchins be ranked in a linear order and what is the degree of hierarchical linearity?

We predicted that rank order among adult individuals would be linear since like Old World monkeys with highly linear hierarchies (e.g., baboons and macaques), capuchins show clear aggressive and submissive behaviours in agonistic interactions.

- (2) Rank acquisition and stabilization:

- (a) How long does it take for a female to acquire a stable rank position within the hierarchy upon reaching sexual maturity?

Since female kin are readily available as social partners, coalitionary support is common, and within-group contest competition for resources is high (Vogel, 2005; Vogel et al., 2007), we predicted that females would quickly acquire a stable rank position.

- (b) Does a female's rank early in life predict her position years later?

We predicted that our study subjects would remain in stable rank positions throughout their lifetimes since (as is true in many species of cercopithecines with stable hierarchies) capuchin females remain resident in their natal groups throughout their lives and should receive consistent support from female kin and from close social partners during competitive interactions across their lifespan.

- (3) Nepotism and matrilineal rank inheritance: Does female rank order follow Kawamura's rules of matrilineal rank inheritance? We explored sub-questions 3b and 3c without any a priori predictions.

- (a) Do females rank adjacent to kin?

Since *Cebus capucinus* are classified as female-bonded and display nepotistic tendencies in various associative patterns (Perry, 1996; Fragaszy et al., 2004) we predicted that females would rank adjacent to close maternal kin.

- (b) Do daughters rank according to youngest ascendancy?

- (c) Do mother's rank above daughters?
- (d) Do daughters occupy similar ranks in their adult lives to those of their mothers?

Once a stable rank position was established, we expected daughters to maintain rank positions in their adult lives similar to those occupied by their mothers.

(4) Hierarchical strength: Are hierarchies strong?

- (a) What proportion of female–female agonistic interactions occurs in the context of food?

We make no prediction here but instead explore the question, with the goal of documenting the proportion of female–female agonism occurring in a feeding context.

- (b) What is the rate of submissive interactions and hierarchical latency to detection?

We predicted that the rate of submissive interactions would increase with the number of adult females per group since members of smaller groups are able to forage simultaneously in smaller areas and may undergo less pressure to compete for resources (Sterck & Steenbeek, 1997). We predicted that latency to detection of white-faced capuchin hierarchies would be short. Clear aggressive and submissive behaviours are exhibited by white-faced capuchins (Vogel, 2005). Furthermore, capuchins engage in coalitional behaviour and although it possibly increases the complexity of competitive interactions and reduces the occurrence of dyadic contests, it likely reinforces existing social rank (Chapais, 1992; Manson et al., 1999).

- (c) How consistent is the direction of agonism within dyads?

We predicted that the direction of agonism would remain consistent and that submission would be directed up the hierarchy in dyadic contests.

(5) Hierarchical stability: Are ranks stable over time?

- (a) Is there a large proportion of tied dyadic relationships?

When social relationships are female-bonded or nepotistic, there is usually consistency in the outcome of competitive interactions and in hierarchical rank patterns over long time spans (e.g., baboons, Hausfater et al., 1982; macaques, Silk et al., 1981; vervets,

Seyfarth, 1980). Since white-faced capuchins have been described as female-bonded based on their patterns of social behaviour (e.g., Fragaszy et al., 2004), we predicted that long-term rank consistency is likely and would result in few, if any, tied relationships.

(b) How often does female group membership fluctuate?

We predicted that female group membership would remain stable since female dispersal and death/disappearance are relatively uncommon.

(c) What is the rate of rank change over time?

Similar to many resident-nepotistic cercopithecines, capuchin females remain with kin in their natal group throughout their lifetimes. Therefore, social relationships should be well known and reinforced during competitive interactions through social support (particularly with close-kin who acquire indirect fitness benefits). We predicted that dyadic relationships formed by capuchin females in our population would remain constant and stable and would exhibit few changes unless major alterations in female group membership occurred.

Methods

Study site and subjects

We collected focal animal data for this study from January to May 2008 in Sector Santa Rosa of the Area de Conservación Guanacaste, Costa Rica. This area consists of 108 km² of seasonal tropical dry deciduous forest (Fedigan & Jack, 2001). Average annual rainfall is 1472 mm (Fedigan & Jack, 2001) with a dry season extending from mid-December until mid-May. We collected data on reproductively mature females (≥ 5 years; Carnegie et al., 2005), that in this study we refer to as adults, from three study groups: LV, CP and GN. We identified individuals based on age, sex, body size and distinguishing features such as facial structure, skin pigmentation, hair coloration and scars. Group size (including all age/sex classes) ranged from 18–33 individuals (LV 18–19, CP 18–19, GN 26–33). The number of adult female study subjects for each group was 5, 7 and 10, respectively, totalling 22 individuals. We did not include males in this study since socio-ecological theory

is fundamentally based on female relationships and competition and suggests that males and females compete for different resources (males compete for females and females compete for resources) likely resulting in different dominance structures. We also excluded juveniles and infants (<5 years old) as they are too young to have established dominance within the group and rank is likely dependent upon the mother's rank (Kawai, 1958).

The 22 years of demographic and dominance data available in the Santa Rosa database (Fedigan, unpubl.), as well as variation in the number of females in LV, CP and GN groups during our behavioural study, allowed us to compare long-term stability and the effects of the number of females on female–female social behaviour. Dominance hierarchies have been constructed on an annual basis for LV and CP over the past 19 and 22 years, respectively, and these were used in our analyses of rank acquisition and stabilization, rank order patterning, and hierarchical stability but not in our analyses of linearity and hierarchical strength. One caveat for the use of the long-term data in some analyses is that although only dyadic agonistic behavioural data were included, the exact set of submissive behaviours used to construct each hierarchy in past years varied, and did not always include all the behaviours (e.g., supplantation, cower, avoid, grimace, flee) used in our construction of dominance hierarchies for 2008. However, because frequency and direction of submissive behaviours rather than rates are used to construct dominance hierarchies, problems associated with using different behavioural subsets per annum were minimized.

Data collection

We followed study groups on a rotational basis for approximately one week per group, for a total of three weeks of data per month (22 focal individuals, 331 focal hours (LV 79, CP 112, GN 140); 714.27 h of observational contact). We collected behavioural data 5 days per week, 10–12 h/day, using a PSION Workabout hand-held computer. We used a digital voice recorder to collect data when behavioural interactions occurred too rapidly to be collected on PSIONs, such as in the case of intense aggression.

We collected 10-min continuous-time focal animal samples to record all behavioural states and events, as well as interactants involving the focal female. Instantaneous scan samples were recorded at 2.5-min intervals during focal follows to record social states and proximity behaviour. We collected

ad libitum data opportunistically for vocalizations (e.g., signalling fights) and intragroup agonism. We used the following rotational rules to select focal females randomly, sample individuals equally each day, and ensure sampling independence: (a) each focal but one must be sampled before moving to the next round of sampling; (b) one focal can be skipped within a round until located if she cannot be found after sufficient search effort or is suspected to be absent from the group; (c) a focal cannot be sampled if she interacted with the previous focal during the last five minutes of the previous follow; and (d) a focal cannot be sampled if she was within five meters of the previous focal in the last scan sample of the previous follow (Perry, 1996).

Variables and analyses

We determined a rank order for each group based on the direction of agonistic dominance interactions among dyads. We considered a dominance interaction as a submissive behaviour, usually but not always following aggression from another individual (i.e., supplantation, avoid, cower, grimace and flee behaviours). Definitions for each submissive behaviour are shown in Table 1. These behaviours are commonly used to determine dominance in dyadic contest situations among primates since a clear 'winner' and 'loser' can be determined within dyadic agonistic behavioural sequences. We constructed dominance matrices for females in each group based on the outcome of these interactions.

To determine the degree of hierarchical linearity we performed a dominance matrix analysis on constructed square matrices of dyadic submissive

Table 1. Definitions of submissive behaviours used to construct dominance matrices for female white-faced capuchins.

Behaviour	Definition
1. Avoid	Actively moving away from another individual as they approach proximity (5 m)
2. Cower	Motion to shudder or withdraw from another individual, often forming a crouched posture
3. Grimace	Horizontally widening of mouth and tensing of lips; teeth are exposed
4. Flee	Rapidly moving away/running from another individual to a position outside immediate proximity (>5 m)
5. Supplant	Approaching within proximity (≤ 5 m) and taking the exact place of another individual at a food or social resource; individuals need not come into contact

interactions using Landau's modified index (h'). This index corrects for 'unknown' relationships (i.e., relationships in which individuals do not have any recorded submissive interactions) or tied relationships (i.e., relationships in which individuals have an equal number of directed submissive behaviours) and is a common statistical measure used to assess the degree to which the hierarchy reflects the transitivity of dyadic relationships (de Vries, 1995). Landau's index varies from 0 (absence of linearity) to 1 (complete linearity). We interpreted values along this continuum according to the following categories: weak (0–0.5), moderate (0.5–0.8) and strong (0.8–1.0) linearity. We calculated the percentage of unknown relationships as the number of female–female dyads for which there were no submissive interactions divided by the total number of female–female dyads for that group.

We investigated rank acquisition and stabilization using long-term data on LV (1990–2008) and CP (1986–2008) groups. First, we determined the amount of time it takes for a female to acquire a stable rank position (calculated as the percentage of individuals dominated) within the hierarchy. We considered the latency to adult rank stabilization as the amount of time between a female's entry into the hierarchy at five years of age until the first year of a time period where rank position is maintained (unchallenged or challenged without resulting fluctuation) for at least three years (relative to females present at maturation and excluding fluctuation in rank position caused by entry of newly maturing females during rank stabilization). To determine if a female's earliest stable rank in adulthood predicted her rank later in life, we calculated the strength of correlation between a female's first 'stable rank' and her rank in the final year she was studied using a Spearman's rho correlation analysis. We analyzed matrilineal rank inheritance patterns using long-term data collected on LV and CP groups from 1997–2008 when maternal relatedness for all females within the study groups was known, excluding immigrants (see Figure 1 for genealogies). We determined the proportion of sister–sister dyads for which the older sisters outranked younger sisters and mother–daughter dyads for which the mother outranked her daughter. Next, we determined if a female occupied a similar rank during adulthood to that occupied by her mother by determining the strength of correlation between a daughter's rank (percentage of individuals dominated) and the mother's rank using a Spearman's rho correlation analysis. Both the mother's and daughter's ranks at the age of nine years were used in this calculation since (1) a female's rank is probably well established at this age, as

the female has likely given birth to at least one infant, (2) it is unlikely for a female to have fallen in rank as a result of aging at this age and (3) this age provided the largest dataset of mother–daughter dyads with known maternal relatedness during the observation period.

A strong hierarchy is one that is regularly expressed through submissive interactions. We assessed three social indicators of hierarchical strength. First, since the occurrence of agonism during feeding is common among species with strong dominance hierarchies (Isbell & Young, 2002), we measured the percentage of dyadic agonism that took place in the context of feeding (out of all agonistic interactions for which the context could be determined). We recorded the context of agonistic interactions as either ‘resource related’ (i.e., aggression or submission occurring at a water source or in a tree while the group was feeding on a food item such as fruit, insects, or vertebrates) or ‘social’ (i.e., aggression or submission occurring while the group was resting or socializing in the absence of a contestable food resource). Second, we looked at the rate of dyadic submission among females in two different ways. We calculated rates of submission (per female’s focal hours) as the total number of submissive behaviours given or received by the focal. Using a one-way ANOVA and Tamhane post-hoc comparison tests to account for unequal group sizes (SPSS, 2007), we compared values across groups to determine if submission rates varied according to the number of adult females in a group. Hierarchical ‘latency to detection’ was then calculated by determining the total hours of observation needed to place females confidently into a dominance hierarchy (Isbell et al., 1998). We were confident that we reached the proper latency time at the point when the hierarchy matched the rank order that persisted for the remainder of the study, following Isbell and Young (2002). We accounted for the variance in number of adult females in each group by dividing the observation hours by the number of females to produce an average latency time per female for each study group (Isbell et al., 1998; Isbell & Young, 2002). Short latencies to detection are characteristic of groups with strongly enforced dominance hierarchies. Third, we used the directional inconsistency index to test the asymmetry of agonism; that is, the percentage of all submissive interactions that were directed in the less frequent direction within dyads (de Waal, 1977). This measure has been proposed as a good indicator of hierarchical strength that also indicates the stability of female–female relationships (Isbell & Young, 2002).

We assessed hierarchical stability over a 22-year period via analysis of annual dominance hierarchies (1986–2008) collected on LV and CP groups. We also inferred the stability of dyadic relationships within each group during the 2008 field season by calculating the proportion of dyads that exhibited ‘high-value tied’ relationships (at or near a 50/50 distribution of submissive behaviours occurring in both directions). The latter are indicators of hierarchical instability since the presence of tied dyads might be a sign of undecided relationships and contested rank positions (Izar et al., 2006). Using longitudinal data, we calculated rates of change in female membership as (1) Female Entry = E/Y , where E is the number of times females entered the group and Y is the number of total years the group was studied and (2) Female Departure = D/Y , where D is the number of times females left the group and Y is the number of total years the group was studied. To assess the stability of female ranks, we calculated the average annual rank change per female (Cheney et al., 1988) for females that were present in the group for more than one year according to the following formula: Rank Change = N/Y , where N is the total number of rank changes for an individual female and Y is the total number of years the female was present in the group. We then calculated an overall mean annual rank change that included all females. We considered a rank change as an ‘active’ movement up or down the hierarchy (i.e., resulting from challenge by an adjacent individual rather than the outcome of a disappearance/death or a shift up due to an individual entering the hierarchy below without known dispute).

Dominance matrix analyses were performed using Noldus MatMan 1.0 (Noldus Information Technology, 1998). All other analyses were conducted using SPSS 16.0.1 for Windows. We considered all results of statistical tests significant at $p \leq 0.05$.

Results

We were able to place all females into a rank order either above or below another female without discrepancies. Avoids accounted for the majority of recorded dominance interactions (40.6%). Cowers, supplantations and flees were less common (16.4, 17.6 and 22.4%, respectively) and grimaces occurred infrequently (3.0%). Actor/recipient matrices (Tables 2–4) show the frequency of submission for each study group as well as the resulting rank

Table 2. Dominance rank of adult female white-faced capuchins and Actor (row)/Recipient (column) matrices constructed using the direction of submissive interactions (avoid, cower, grimace, flee, supplantation (transposed)) for LV group.

Rank	ID	KL	DL	BB	SL	CH
1	KL	*	0	0	0	0
2	DL	7	*	0	0	0
3	BB	3	1	*	0	0
4	SL	1	1	1	*	0
5	CH	4	2	1	3	*

Table 3. Dominance rank of adult female white-faced capuchins and Actor (row)/Recipient (column) matrices constructed using the direction of submissive interactions (avoid, cower, grimace, flee, supplantation (transposed)) for CP group.

Rank	ID	SI	SA	ED	TI	KI	SE	ZA
1	SI	*	0	0	0	0	0	0
2	SA	3	*	0	0	0	0	0
3	ED	9	4	*	0	0	0	0
4	TI	6	6	7	*	2	0	0
5	KI	14	8	1	4	*	1	1
6	SE	9	4	8	1	3	*	1
7	ZA	9	3	0	2	7	4	*

order among adult females. We recorded 296 submissive interactions during 714.26 h of observation (LV: 24 interactions/191.6 h; CP: 117/228.13; GN: 155/294.53). We recorded 338 aggressive interactions (201 during focal follows and 137 from ad libitum sampling). The rate of aggression in all three groups was less than one interaction per hour (LV: 0.30; CP: 0.58; GN: 0.80).

What is the degree of hierarchical linearity?

Landau's linearity index (h') scores were significant and highly linear for CP ($h' = 0.776$, $p = 0.001$) and GN ($h' = 0.893$, $p = 0.016$) groups. Although Landau's linearity index was high for LV group, h' was not significant ($h' = 1.000$, $p = 0.113$). This is probably due to the small sample size ($N = 5$)

Table 4. Dominance rank of adult female white-faced capuchins and Actor (row)/Recipient (column) matrices constructed using the direction of submissive interactions (avoid, cower, grimace, flee, supplantation (transposed)) for GN group.

Rank	ID	LY	MX	MV	PT	LL	RS	FL	MW	RM	LV
1	LY	*	0	0	0	0	0	0	0	0	0
2	MX	0	*	0	0	0	0	0	0	0	0
3	MV	0	1	*	0	0	0	0	0	0	0
4	PT	5	12	4	*	0	0	0	0	0	0
5	LL	1	2	0	3	*	2	1	0	0	0
6	RS	2	4	7	9	5	*	0	0	0	0
7	FL	2	2	3	7	3	2	*	0	0	0
8	MW	3	0	1	6	0	1	1	*	0	0
9	RM	4	5	0	6	6	6	0	6	*	0
10	LV	7	4	4	10	5	0	1	2	0	*

in LV, which limited the power of linearity analysis (six individuals are required to achieve statistical significance and to eliminate the mathematical possibility that the determined hierarchy was obtained by chance) (Appleby, 1983). The percentage of unknown relationships was very low for LV and CP groups (LV, 0/10 dyads: 0%; CP, 1/21 dyads: 4.76%) and relatively higher for GN group (9/45 dyads: 20%).

When do rank acquisition and stabilization within the adult hierarchy occur?

Over the 19- and 23-year study periods covered by our study of LV and CP groups, a total of 33 adult females have been observed. Fifteen females matured into adults in their natal groups during observation. Of these, six were removed from the sample (CA, MA, SA, ED, KI, ZA) because, during our study, they were not present in the adult hierarchy for three years after rank acquisition, which is the amount of time required to accurately assess rank acquisition and stability. The mean latency to adult rank stabilization equalled 1.75 ± 0.70 years (range 1–3 years) for the eight females who achieved stable rank positions during our long-term study period (KL, DL, CH, SE, NY, PU, SI, SL). The fifteenth female (TI) that we observed to mature into the adult hierarchy has failed to maintain a stable rank position for a period of more than two years although she has remained mid-ranking

throughout adulthood. Following Pusey et al.'s (1997) approach, we investigated whether a female's early rank predicted her rank later in adulthood, using females that had been studied at least three years. We found a strong correlation between the stabilized rank a female acquired early in her adult life (6 years old) and her position in the final year she was studied (range 9–19 years old) (Spearman's $\rho = 0.887$, $N = 7$, $p = 0.008$, mean number of years observed = 8.7). It should be noted that the length of interval between 'first stable rank' and 'final year studied', as well as the age of females during the final year studied, differs across analyzed females. And if rank falls with old age (Perry et al., 2008), the 'final year studied' measure could tap different processes in those females that were elderly in the final year studied versus those that were not. Nonetheless, the correlation between stabilized and final assessed rank was strong.

Five adult females entered the hierarchies of CP and LV groups through immigration. Only two of the immigrant females remained in the study groups for more than 3 years (FE 6 years and P1 4 years) making it difficult to determine dominance patterns among this category of females. However, both of these immigrant females acquired a low rank position within one year of entering into their respective groups and held a stable low-rank position for the remainder of their time in the group, suggesting that related allies may be important to ascend the hierarchy. It is possible that immigrant females did not have the necessary support to successfully compete amongst the natal females.

Does female rank order follow Kawamura's rules of matrilineal rank inheritance?

Almost all individuals with maternal kin simultaneously present in the hierarchy ($N = 14$, 3 matrilineal in LV and 3 matrilineal in CP) ranked adjacent to maternal kin in both groups. The one exception was KI, who was the youngest adult female in the CP group and probably had not fully established or stabilized her rank. Her rank increased between 2007 and 2008 and if this trend continues it is assumed she will settle into rank position below her older sister (ED) once her rank is fully established, thus following the rank positioning pattern for this population. Daughters do not rank according to youngest ascendancy. In 8 of 8 (100%) sister–sister dyads, older sisters outranked younger sisters for all years where they were present together in

the hierarchy with the exception of one dyad during one year (ZA ranked above TI her first year in the hierarchy but TI's rank was not yet considered stable). Of the five mother–daughter dyads present during this time period, mothers outranked daughters in one dyad (BB–CH), ranks of both mother and daughter were considered unstable for two dyads (BB–SL and SE–ZA), and a rank reversal occurred in which the daughter overtook the mother's position in two dyads (LI–NY and SE–TI). In both cases of rank reversal, mothers were at least 14 years old. LI (~20 years old) disappeared the year after NY took over the alpha female position. There was a strong correlation between the daughter's rank and her mother's rank at the same age (nine years old) (Spearman's $\rho = 0.662$, $N = 10$, $p = 0.037$). Only five of 15 (33.3%) mothers were still present in the hierarchy when their daughters acquired a rank position.

Are hierarchies strong?

A high proportion of agonistic interactions occurred in the context of food. A total of 230 agonistic interactions with known context were recorded across LV, CP and GN groups. A one sample χ^2 test showed that a significantly higher amount of agonism occurred in a resource related (146/230 = 63.5%) versus social context (84/230 = 36.5%), indicating strong hierarchies ($\chi^2_1 = 16.713$, $p < 0.001$).

The average overall rate of submission across groups was 0.53 ± 0.36 interactions/focal hour (Mean, LV: 0.216 ± 0.15 ; CP: 0.751 ± 0.231 ; GN: 0.634 ± 0.40). Rates of submission varied significantly across the three study groups (ANOVA: $F_{2,19} = 4.680$, $p = 0.022$). Tamhane's post-hoc comparison indicated that the smallest group (LV) exhibited significantly lower rates of submission than either CP ($p = 0.002$) or GN ($p = 0.035$), and that rates of submission were not significantly different between CP and GN groups (Figure 2). These data satisfy the homogeneity of variance and normality assumptions of the ANOVA. The number of observational hours needed to place females confidently into a dominance hierarchy (LV 99.32 h; CP 148.55 h; GN 219.92 h) increased as the number of adult females within a group increased. However, when latency to detection times for each group were corrected for the number of females (LV = 19.86, CP = 21.22, GN = 21.99), we found a consistent value across groups of approx. 21 h/female (mean = 21.02, SD = 1.08).

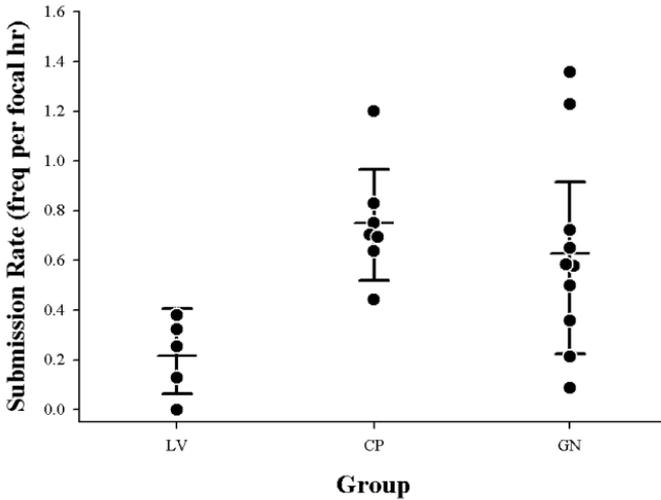


Figure 2. Submission rates calculated as frequency per focal hour for each female in each group (LV, $N = 5$, CP, $N = 7$, GN, $N = 10$). The original data for each group are plotted along with the means (middle bars) and 95% confidence interval (top and bottom bars). Submission rates varied significantly among the females in the three groups (ANOVA: $F_{2,19} = 4.660$, $p = 0.022$). Tamhane's post-hoc comparison indicated that submission rates in the smallest group, LV, were significantly lower than in each of the two larger groups, CP ($p = 0.002$) and GN ($p = 0.035$).

The direction of agonism within dyads was consistent. For LV, all dyads exhibited solely unidirectional submissive interactions where the higher ranked individual always supplanted or received submission from the lower ranked individual (DII = 0%). For CP, 95.24% of relationships were known. Of the known relationships, 20% exhibited bidirectional submissive interactions (4 of 21 dyads: lower ranking individuals) resulting in an increased DII of 4.27%. For GN, 80% of the dyads were known, and 5.56% of dyads exhibited bidirectional submissive interactions (2 of 45 dyads: mid-ranking individuals including LL, who was common to both dyads), resulting in a DII score of 1.94%.

Are ranks stable over time?

None of the dyadic relationships across the three study groups were tied, providing evidence for stable relationships among females. The rate that females entered the adult hierarchy per group each year through immigration or maturation to adult status based on long-term data from LV and CP (19 and 23 years, respectively) was 0.9 females/year and the rate they left through

emigration or death/disappearance was 1.1 females/year. We determined that the average number of rank change events per female per year for LV was 0.287 (ranging from 0 to 0.632, $N = 10$) and for CP it was 0.510 (ranging from 0 to 1.333, $N = 17$). Thus, the overall annual rank change per female was 0.427. At this rate, one rank change per female as a result of active challenge is expected every 2.34 years.

Discussion

Hierarchical linearity

Our results for all three study groups indicate that female white-faced capuchin hierarchies are linear. The low percentage of unknown relationships in LV and CP groups contributed to reliable construction of rank orders. Linearity was also high in GN despite a relatively higher number of unknown relationships. In addition to the presence of unknown relationships, the slightly bidirectional relationships in dyads where rank disparity between individuals is low may explain the slight drop in the degree of linearity from perfect transitivity ($h' = 1.0$) in our two larger study groups (CP and GN). In CP, four of five (80%) bidirectional submissive interactions (i.e., interactions that included submission of a higher ranking female towards a lower ranking female) included KI, who has not yet established a set rank position. All bidirectional submissive interactions (five in CP and three in GN) were between females separated by two or fewer rank positions. Landau's h' scores from this study period were slightly higher than those reported for white-faced capuchin groups with the same or similar numbers of females during comparable seasonal conditions at Lomas Barbudal, a neighbouring field site ($h' = 0.5$, $p = 0.13$; Perry et al., 2008). Between-site variability may simply reflect differences in group composition and relationship dynamics within 'low rank disparity' dyads, or from a socio-ecological perspective, may indicate slight differences in social response to competition and food availability between the two study populations.

The linearity of a hierarchy is related to female dispersal patterns and social structure since the formation of strong social bonds can help to reinforce and maintain dominance relationships (Chapais, 1992). The linearity indices for this population are consistent with those found for other female philopatric species that exhibit similarly high levels of association,

strong coalitionary behaviour and nepotistic tendencies (van Schaik, 1989; Isbell, 1991; Sterck et al., 1997). Baboons and macaques are examples of highly studied 'resident-nepotistic' Old World monkey species that exhibit similar behavioural patterns as well as linear hierarchies (Samuels et al., 1987; Thierry, 2007). Among the platyrrhines, other capuchin species also live in female philopatric, male dispersed societies in which females exhibit frequent coalitionary activity and linear hierarchies (e.g., tufted capuchins (*Cebus apella nigrurus*) Janson, 1985; Di Bitetti, 1997; wedge-capped capuchins (*Cebus olivaceus*), O'Brien, 1993). Also, *Saimiri boliviensis* (another female-philopatric, male-dispersed platyrrhine, closely related to *Cebus*) display strong, linear dominance hierarchies in response to competition for clumped resources (Boinski et al., 2002).

Rank acquisition and stabilization

Although very little is known about the transition from adolescence to adulthood in white-faced capuchins, a female's rank seems to be dependent upon her mother's rank until she is sexually mature. As females begin to cycle around 5 years of age (Fedigan & Rose, 1995; Fragaszy et al., 2004; Carnegie et al., 2005), they also begin to acquire a position in the dominance hierarchy among other adult females. For the females that we were able to study over a sufficient period of their transition into adulthood, the process of acquiring a stable position in the hierarchy takes one to two years and the resulting position is likely to remain steady throughout the female's lifetime/residency within the group. Thus, we suggest that initial rank acquisition has lifetime consequences and may reflect underlying structure and stability in the rank order of matriline, as well as immediate social relationships.

A pattern of rank acquisition and stability such as this might have important implications for health and fitness. If higher ranking females gain priority of access to usurpable resources, consistency in dominance rank over time could result in a greater impact of dominance on lifetime fitness (reviewed by Fedigan, 1983). Certainly, rank order in many species of OWM (e.g., baboons, *Papio* spp.: Hausfater et al., 1982; Altmann & Alberts, 2003) is consistent throughout an individual's lifetime and high rank has been correlated with increased fitness (including increased infant survival, shorter inter-birth intervals and lower age of sexual maturity for offspring, Pusey et al., 1997) and reduced stress (Sapolsky, 2005). However, a previous study

of white-faced capuchins at Santa Rosa did not find an effect of female rank on fitness in terms of reproductive output, probably due to confounding influence of male reproductive strategies (e.g., group take-overs and infanticide) on the long-term reproductive success of females (Fedigan et al., 2008). While male strategies can lower overall reproductive success of females during times of instability and after male takeovers, high dominance rank may still have a positive impact on individual health during periods of stability, reducing psychological and physiological stress and improving reproductive success on a smaller time scale. A comparison of reproductive output during periods of stability and instability, as well as measures of health such as nutritional intake, body weight and condition, and stress (i.e., glucocorticoid levels) in white-faced capuchins would further test this suggestion. Also, research regarding factors influencing the acquisition of rank such as coalitionary support from others, most importantly mothers and full-siblings, would help us better understand rank order patterns in relation to dominance and inclusive fitness benefits in this species.

Nepotism and matrilineal rank inheritance

Dominance relationships among females in LV and CP groups were nepotistic and females ranked adjacent to kin, yet rank order among sisters did not follow Kawamura's principle of youngest daughter ascendancy. Instead, once a female established her rank within the hierarchy, she tended to rank according to her age, with older sisters ranking higher than younger ones. This pattern of rank order among white-faced capuchins suggests two things. First, age and individual attributes such as size may play a role as important as nepotism in the organization of capuchin hierarchies; measures of body size and weight would help to clarify this finding. Second, mothers may only infrequently support daughters in agonistic interactions (e.g., against their sisters: only 5 of 15 (33.3%) mothers were still present in the hierarchy when their daughters acquired a rank position) and/or that an individual's dependent rank on her mother might diminish before rank establishment in the adult hierarchy commences. Accordingly, when a young capuchin female reaches an age at which she needs to compete for resources, she must work her way up the hierarchy by challenging those with previously established ranks to develop dominance relationships and solidify her new status. Effectively, such rank challenges and changes may occur until a female obtains a rank position below but adjacent to her sibling(s). A possible reason

for hindrance of further rank ascendancy within the hierarchy is that once positioned adjacent to kin, a female would be unlikely to overtake her maternal kin and ascend the hierarchy any further due to strong established social bonds and potential lack of social support. This pattern of rank acquisition differs from many OWM species (e.g., chacma baboons, *Papio ursinus*: Cheney, 1977; Japanese macaques: Kawai, 1958; rhesus macaques: Berman, 1983) where the role of the mother in acquisition of social status is much greater. Detailed studies of social behaviour, including coalitionary behaviour, before and during rank acquisition are needed to better understand patterns of rank ascendancy.

There were not enough instances where either (1) a mother was present during the same time period as her daughters or (2) ranks were stable enough to make a valid assessment of patterns of mother-daughter rank order. In both cases of mother-daughter rank reversal, mothers were at least 14 years old. Past studies of macaques have found an effect of age on social behaviour that varies by species and degree of social withdrawal (e.g., Japanese macaques: Pavelka, 1990; toque macaque, *Macaca sinica*: Ratnayake, 1994; long-tailed macaque: Veenema et al. 1997). Veenema et al. (1997) found that older individuals (≥ 14 years) spent less time socializing and that lower ranking individuals were affected more by age than higher ranking individuals. Little is known about the effect of age on sociality in white-faced capuchins. Although age does not seem to affect social behaviour in captive tufted capuchins (Fragaszy et al., 2004), it is possible that age might cause social withdrawal and an ensuing drop in rank position for old females in wild populations where ecological pressures impacting competition and social behaviour are greater. Perry et al. (2008) presented evidence that rank declines with age for two females in a neighbouring population of white-faced capuchins. However, a larger sample size from both the Santa Rosa and Lomas Barbudal study populations is needed to draw firm conclusions regarding the relationship of age and rank.

Nonetheless, our results suggest that nepotism plays a key role in the structure of female hierarchies in the capuchins at Santa Rosa. Despite deviation of the capuchin rank patterning from Kawamura's 'youngest daughter ascendancy' rule, and the ambiguous results regarding mothers ranking over their daughters, the importance of nepotistic support among white-faced capuchins is still apparent since maternal kin do acquire rank adjacent to one another.

Hierarchical strength

Measures of hierarchical strength indicate that white-faced capuchins exhibit strong dominance hierarchies. A significant percentage of agonism occurred in a resource-related context, indicative of a strong hierarchy. The rate of submission was significantly greater in the two larger groups (CP and GN) than LV group. However, the latency to detection was consistent for all three groups at approx. 21 h/female ($N = 22$). This is a very short latency relative to other monkey species such as vervets (46 h/female, $N = 9$) or patas (51 h/female, $N = 15$) (Isbell & Young, 2002), suggesting that white-faced capuchins have stronger or more highly expressed dominance hierarchies compared to these Old World monkey species. The low directional inconsistency scores (<5%) reported for all three groups in this study provide another indicator of strong dominance hierarchies. This low range of DII scores compare to scores for a number of macaque species (e.g., *Macaca thibetana*, DII scores 0–5%) reported as having strong hierarchies with despotic dominance relationships (Berman et al., 2004). Baboons (*P. cynocephalus*: <1%, Hausfater et al., 1982; *P. anubis*: 3.2%, Barton & Whiten, 1993) and vervets (*Ch. aethiops*: 0%, Isbell & Pruett, 1998) show very low levels of directional inconsistency in dominance behaviours as well. The directional inconsistency index measure is said to correlate with hierarchical stability (Isbell & Young, 2002), as hierarchies with fewer dominance reversals against the hierarchy tend to be more stable over time. To date, no quantitative assessment of hierarchical strength has been performed for other New World primate species.

Hierarchical stability

Our analyses of stability to date indicate that female white-faced capuchin hierarchies are stable. Dominance relationships are either decided or avoided altogether; no relationships were tied or heavily disputed during this study period, which would have been indicated by a high level of bidirectional submission within a dyad. However, a closer look at factors influencing linearity shows that a few bidirectional cases of submission occurring among dyads of low rank distance may indicate low-grade instability and decrease the degree of linearity from perfect transitivity.

Adult female group membership in this population changes by approximately two females per year and females are likely to change rank every 2.34 years. Changes in group membership are likely to provide a constant

low-grade disruption of hierarchical stability contributing to rank change, since each year females present in the hierarchy fill positions left by exiting females and females reaching maturation will enter and challenge others until rank has been established. Despite small-scale fluctuations in rank over the course of long-term study for this population, there were no changes in the ordering of matriline over the past eight years in CP and ten years in LV (despite one male takeover in CP and three in LV). This lack of change indicates considerable stability in dominance relationships among female white-faced capuchins in the face of low-grade fluctuation in females or more drastic changes in male composition and membership. Monitoring for more rapid changes in rank order or larger changes such as reversals of matriline may be crucial for identifying disruptive pressures contributing to dominance instability. Observations of changes in dominance relationships may also be an important step in evaluating the adaptive significance of female dominance rank for capuchins.

In conclusion, we found that female white-faced capuchins form highly linear hierarchies. Rank order patterns in our study population suggest that both nepotistic behaviour and individual qualities such as age contribute to hierarchical organization; sexually mature females quickly acquire rank positions adjacent to kin and below older sisters. Females also rank in a position similar to their mothers, even when rank was acquired when mothers were no longer present in the group. The social relationships formed by young females as they enter the adult hierarchy likely contributes to long-term hierarchical stability, as it does in *Cebus olivaceus* (O'Brien & Robinson, 1993). The formation of strong hierarchies among female white-faced capuchins suggests that dominance is clearly and regularly asserted by dominants toward subordinates in competitive situations. The differential costs of dominance across ranks (i.e., high versus low) are likely more extreme in species with linear and strong hierarchies like *C. capucinus*, where a clear rank order is strictly enforced. Demographic changes such as alpha male takeovers or low-level on-going fluctuation in female membership do not seem to greatly affect hierarchical stability. A combination of changes (e.g., male takeover and the simultaneous loss of more than one female) may be required to destabilize female dominance relationships in this population.

Results from this study of hierarchical structure are congruent with the linear and stable hierarchies reported for other populations of *C. capucinus* and for *C. olivaceus* (O'Brien & Robinson, 1993; Perry et al., 2008). However,

in brown capuchins (*C. apella*), rank reversals of matriline following alpha male takeover have been observed despite the formation of linear hierarchies among females in this species (Janson, pers. commun.). Alpha male–female social bonds do not seem to be as strong in *C. capucinus* as in *C. apella*, which may be one reason why alpha male takeovers have a greater impact on female hierarchical stability in *C. apella*.

In sum, we suggest that the dominance hierarchy patterns we have documented in white-faced capuchins largely support socio-ecological predictions previously developed for resident-nepotistic cercopithecine species with high intra-group competition (e.g., baboons, macaques and vervets). That is, our female philopatric study subjects display characteristics of strong female–female social relationships with nepotistic and linear dominance hierarchies. Isbell & Young's (2002) suggestion to include more detailed measures of hierarchical strength and stability in dominance assessment has helped to expand the comparative framework with which to test behavioural responses to social and ecological conditions across primate species. Using these measures, we found that white-faced capuchins display strong and stable dominance hierarchies, akin to resident-nepotistic cercopithecines. That these similarities occur despite phylogenetic differences, suggests that ecological factors such as resource characteristics may influence competitive strategies and dominance behaviour. The findings from our study regarding dominance characteristics among female white-faced capuchins opens the door to more extensive investigation of the costs and benefits associated with dominance status and how they relate to other aspects of socio-ecology. Two approaches that would further advance studies of dominance and socio-ecology across taxa would be the expansion of dominance studies to additional New World primate species and the inclusion of more detailed ecological measures in these studies, as suggested by Koenig & Borries (2006).

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