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Primate Life Histories, Sex Roles, and Adaptability

Essays in Honour of Linda M. Fedigan

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Chapter 6

Alpha Male Capuchins (*Cebus capucinus imitator*) as Keystone Individuals

Katharine M. Jack and Linda M. Fedigan

Abstract A keystone individual is defined as an individual that has a disproportionate impact on group dynamics relative to its representation in the population. Here we use over 30 years of behavioural, physiological, paternity, and demographic data collected on the Santa Rosa, Costa Rica, capuchin population to address the question of whether or not alpha male white-faced capuchins (*Cebus capucinus imitator*) are keystone individuals. Within groups of white-faced capuchins, the alpha male is easily distinguished from other adult males. He is usually of prime age (10–15 years) and often the largest male due to his pronounced secondary sexual characteristics. He is the most central adult male and the recipient of the highest rates of grooming. He is also the most active participant during encounters with predators and extragroup individuals. Using naturally occurring dispersal events, we assess the impact of the *removal* of an alpha versus subordinate adult male on group dynamics, specifically infant mortality. We found that infant mortality following the removal of an alpha male was more than double the rate observed following the removal of a subordinate adult male. The removal of an alpha male has additional consequences for group success, individual life histories, and population conservation that extend far beyond the immediate aftermath of an alpha male replacement. Based on these findings, we conclude that alpha male white-faced capuchins are keystone individuals, and future research should focus on identifying the factors that enable some males to attain alpha status while others live out their lives as subordinates.

Keywords Keystone individual · Alpha male · Dominance · Demography · Infant mortality

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6.1 Introduction

> We suggest that the alpha animal in primate groups may not be simply one rank higher than the beta animal. Instead, the alpha animal may behave in a distinctive pattern made up of a variety of related behaviors pertaining to control of the interactions within the group and management of the relationship between the group and external factors. (Gould et al. 1997, p.411)

More than 20 years ago, in their comparative analysis of alpha male ring-tailed lemurs (*Lemur catta*) and white-faced capuchins (*Cebus capucinus imitator*), Gould et al. (1997) recognized that the behaviour of alpha males in these two species was discernably different from that of subordinate males. While their study focused on male vigilance behaviour, they proposed that there are a number of behaviours that enable us and, more importantly, other group members to discriminate the difference between alpha and non-alpha individuals. Earlier studies of primates also recognized alpha males as distinct from subordinate group males. For example, based on his experimental studies of male capuchins (*Cebus albifrons*) and macaques (*Macaca mulatta*), Bernstein (1964 and 1966) suggested that alpha males exhibit a "constellation of behaviours" and when/if this male is removed by either death or experimentation, another male will quickly begin to display these same behaviours.

The existence of *highly influential individuals* that have a large impact on the behaviour and/or success of conspecifics, such as the alpha males described above, has been since noted in many species of social animals (reviewed by Modlmeier et al. 2014). In social insects engaging in collective behaviours, for example, the "behavioural type" of certain individuals (e.g. highly aggressive) has been shown to cause behavioural responses in other group members; these triggered responses can impact prey capture rates in social spiders (*Stegodyphus dumicola:* Pinter-Wollman et al. 2017) or colony movement rates in ants (*Diacamma indicum*; Sumana and Sona 2013), both of which can profoundly affect colony fitness. In species of social mammals that form dominance hierarchies, the alpha male and/or female in a social group will have preferential access to resources that can not only impact social relationships within the group, but can affect the physiology and fitness of other group members (Sih and Watters 2005). In other taxa, influential individuals may have different labels and different roles. In pig-tailed macaques (*Macaca nemestrina*), for example, certain individuals are referred to as *conflict mangers* as they will "police" the group to maintain social order (Flack et al. 2006). In other species some individuals are considered *superspreaders* because of their inordinately high rates of disease transmission (*Oleander aphids*, *Aphis nerii*: Harrison and Mondor 2011), while in bottlenose dolphins (*Tursiops truncatus*), *brokers* are individuals that play a crucial role in maintaining community cohesion (Lusseau and Newman 2004).

Many more terms exist and definitions vary (reviewed by Modlmeier et al. 2014; Pinter-Wollman et al. 2017), though the common feature is that these individuals differentially impact other group members (Modlmeier et al. 2014). In an effort to establish an organizational framework for future research, and to synthesize this topic across fields, Modlmeier et al. (2014) suggest referring to these highly influential individuals as "keystone individuals". Derived from the keystone species concept, which argues that certain species play a unique role crucial to the success of a particular ecosystem (Paine 1969), Modlmeier et al. (2014, p. 55; see also Sih and Watters 2005) define a keystone individual as an "individual that has a disproportionally large, irreplaceable effect on other group members and/or overall group dynamics relative to its abundance".

While the fitness consequences of interindividual trait variation (Bolnick et al. 2003) and the existence of highly influential individuals are not debated, quantitatively documenting the impact of these individuals on a group or population can be problematic, even though it is imperative to informing and expanding this conceptual framework. As such, Modlmeier et al. (2014) outlined a series of methods for detecting the existence of keystone individuals using observational data, controlled manipulations, and/or social network analysis. While the authors state a clear preference for controlled social group manipulation, these methods are not ethical or feasible for most studies of wild primates (Fedigan 2010; MacKinnon and Riley 2010). When using observational data to identify keystone individuals, Modlmeier et al. (2014) suggest collecting descriptions of the behavioural patterns of potential keystone individuals and documenting their effects on group dynamics. If keystone individuals are easily identified, researchers can compare their traits across groups to explore how these traits themselves might be associated with the success of a group (McComb et al. 2011). In some cases, natural experiments wherein the keystone individual is "removed" from the group (e.g. the deaths of aggressive dominant male olive baboons, *Papio anubis*; Sapolsky and Share 2004) can inform our understanding of the impact keystone individuals have on group dynamics, though confounding factors (e.g. change in group size with the removal of the alpha male) may remain an issue.

The concept of keystone individuals was suggested over a decade ago (Sih and Watters 2005) but has seen surprisingly little direct investigation. Interestingly, although Modlmeier et al. (2014) acknowledge the existence of dominant or alpha individuals in social animals as being among the most noticeable examples of keystone individuals, the use of this concept remains largely restricted to the study of collective behaviour in social insects (e.g. Pinter-Wollman et al. 2017 and Pruitt and Pinter-Wolman 2015 on social spiders *Stegodyphus dumicola*). Recognizing the existence of keystone individuals across diverse systems and documenting their impact on group dynamics and success can inform our understanding of the evolution of sociality and cooperative behaviour. In addition, like the keystone species concept, which recognizes particular species whose existence has a far-reaching impact on the functions and survival of the entire biological communities, the keystone individual concept may also help us better understand the impact that the removal of a single, highly influential, individual can have on their group and possibly the population.

In this study, we examine the keystone individual concept using data collected over a 30-year period on the Santa Rosa population of wild white-faced capuchins (*Cebus capucinus imitator*) in Costa Rica. White-faced capuchins are excellent candidates for exploring the keystone individual concept because in this species alpha males are easily recognizable, they behave in a unique way (Gould et al. 1997), and they represent a distinctive life-history stage not experienced by all males (Jack et al. 2014). Following the organizational framework proposed by Modlmeier et al. (2014), we begin with a description of relevant features of white-faced capuchin behavioural ecology (Sect. 6.2) followed by a presentation of our findings to date on the features of alpha male capuchins that distinguish them from other adult males in the population (Sect. 6.3). We then use regularly occurring alpha male replacements and the dispersal of subordinate adult males as natural "removal" experiments to examine the differential impact of these two types of adult males on group dynamics and success, namely, infant mortality (Sect. 6.4). In considering these issues, we explore the significance of alphas as keystone individuals in this species and examine the conservation implications of these findings (Sect. 6.5). Finally, we examine the relevance of the keystone individual concept to our understanding of dominance and make suggestions for future research on this topic (Sect. 6.6).

6.2 General Features of White-Faced Capuchins

Our studies in the Santa Rosa sector of the Área de Conservación Guanacaste, Costa Rica, began in 1983 with demographic, behavioural, ecological, and life-history data collected near-continuously since that time (see Fedigan and Jack 2001, 2012 for detailed history of the project). Santa Rosa is comprised of 108 km^2 of dry deciduous forest and has been federally recognized and protected since 1972. The region experiences extreme seasonal effects, with little to no rain falling during the dry season that extends from mid-December through mid-May and an average of nearly 1500 mm of rain falling during the wet season months (Janzen and Hallwachs 1995; see also Campos 2018, this volume). The Sector Santa Rosa is home to just under 700 capuchins residing in 45 groups (Jack and Fedigan unpublished data), and our long-term research has focused on between two and five groups residing in and around the central administrative area of the park. In addition to our team's research on this species, Susan Perry and her team have been studying a nearby population of white-faced capuchins at Lomas Barbudal, Costa Rica, since 1990 (e.g. Perry et al. 2012), making this one of the most intensively studied species of neotropical primate.

White-faced capuchins are female philopatric and reside in groups comprised of multiple immigrant subadult (6–9 years) and adult males (≥10 years), related adult females, and their offspring (Fedigan 1993). The ratio of adult males to adult females within groups is nearly equal, though a slight bias towards males has been recorded across the Santa Rosa capuchin population (Fedigan and Jack 2011; Fedigan and Jack 2012). Female white-faced capuchins give birth to their first infant at a mean of 6.5 years of age (Fedigan and Jack 2012). The interbirth interval is relatively long (mean = 2.25 years when the prior infant survives) (Fedigan 2003;

Fedigan et al. 2008) in comparison with similarly sized primates, likely because female capuchins continue to nurse their young well into their second year of life (Sargeant et al. 2015). Though births have been recorded during all months, the species is considered a moderately seasonal breeder with most births clustered during the early months of the annual rainy season (May through July) (Carnegie et al. 2011). Females reproduce throughout their lives, and our oldest recorded female to date, followed from birth to death, was just over 23 years of age.

Unlike females who pass directly from the juvenile to adult stage following the birth of their first infant, male capuchins experience a distinctive subadult life-history phase (6 to 9 years of age) during which puberty occurs and they are physically and behaviourally distinct from both juvenile and adult males (Jack et al. 2014). Males do not reach full adult body size until around 10 years of age and only acquire the complete suite of secondary sexual characteristics if and when they attain alpha status within a group (Schoof and Jack 2013; Jack et al. 2014) (see images of adult male capuchins in Fig. 6.1). Male capuchins leave their natal group at approximately 4 years of age (Jack and Fedigan 2004a; Jack et al. 2012) and reside in multiple social groups, at varying dominance ranks, throughout their lives. The oldest male we have recorded from birth is currently 24 years and still an alpha male in one of our study groups (see “Legolas”, Fig. 6.1c).

Alpha male replacements (the changeover in a group’s alpha male; Teichroeb and Jack 2017) are common in this species, though alpha male tenure length is highly variable, ranging from 2 months to almost 15 years in the Santa Rosa population (mean = 3 years; median = 2.3 years, n = 19 complete alpha male tenures; Jack and Fedigan, unpublished data; see Perry et al. 2012 for similar findings in the Lomas Barbudal population). Intragroup male-male relationships are characterized

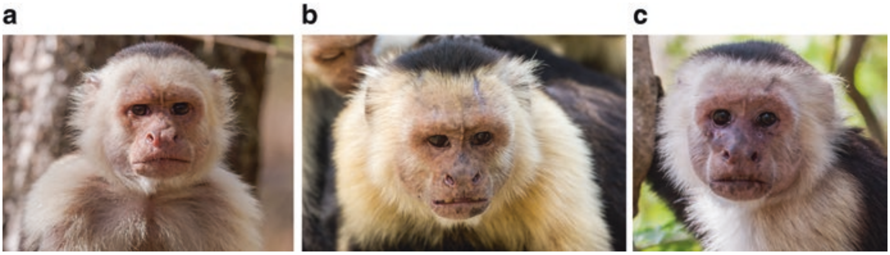

Fig. 6.1 Comparative images of adult male capuchins (Photo courtesy of Fernando Campos). Image a: *Weirdo*, a subordinate adult male white-faced capuchin photographed at ~ 18 years of age who, to the best of our knowledge, never attained alpha status during his lifetime. Scars on the bridge of his nose and above his right eye are evidence of his participation in past male-male aggression. Image b: *Legolas*, an alpha male white-faced capuchin photographed at ~15 years of age. This male became alpha via succession following the disappearance of the group’s long-term alpha. He sports some large scars on his forehead, one of which was the results of a wound incurred shortly before the photograph was taken. The large black mark on the left side of his chin is natural, but many of the other dark marks are the result of past wounds. Image c: *Marmite*, a recently deposed alpha male white-faced capuchin at ~18 years of age. Note canine punctures under both eyes, scars on the forehead, and almost completely darkened face from past wounds

by mutual tolerance, occasional affiliative interactions, and cooperative group defence against predators and extragroup males (Perry 1998a; Jack 2003; Schoof and Jack 2014). Coresident males in Santa Rosa rarely engage in agonistic interactions making it impossible to reliably determine male dominance rank below the alpha level (Schoof and Jack 2013, 2014). However, capuchins are extremely xenophobic, which leads to intergroup interactions characterized by high levels of aggression, particularly among males from different groups (Perry 1996; Fedigan and Jack 2004). Adult male white-faced capuchins usually immigrate into groups by aggressively and cooperatively evicting resident males (Fedigan and Jack 2004), and immigration is the primary way in which they increase their dominance rank (Jack and Fedigan 2004a; Schaebs et al. 2017). Alpha male replacements often result in the eviction of resident males, infanticide and infant disappearances, and the occasional deaths or disappearances of juveniles, adult males, and adult females (Brasington et al. 2017; Fedigan 2003; Gros-Louis et al. 2003).

6.3 How Do Alpha Male Capuchins Differ from Other Group Males?

Although white-faced capuchins can reside in groups as large as 40 individuals and contain up to 13 adult males (Perry 2012), even the most inexperienced observer of animal behaviour would require no more than an hour of direct observation to discern the group's alpha male. As recognized by Gould et al. (1997), there is a suite of characteristics that enable us, and presumably other group members, to easily discern the alpha male from other males in the group. Since that publication, our long-term research in Santa Rosa, and that of Susan Perry and colleagues at Lomas Barbudal, have greatly increased our knowledge of male behaviour and life histories in this species. The behaviour of an alpha male is conspicuous; he is the most vigilant group member, the most active during encounters with predators and extragroup individuals, the most central, and the most groomed; and he is even the recipient of alpha-specific vocalizations. All in all, there is just no mistaking him. Here we present evidence gathered to date that supports our contention that alpha male capuchins differ from other group males based on their physical, behavioural, physiological, and reproductive characteristics.

6.3.1 Looking Like an Alpha Male

The alpha male in a group of white-faced capuchins is generally in his prime (10–15 years of age), usually the largest male in the group (be this from pure body size differences or his constant state of piloerection), and sports the most pronounced secondary sexual characteristics (e.g. exaggerated brow ridges, exaggerated mandibular girth, and wide shoulder girdle) (Schoof and Jack 2013; Jack et al. 2014; Perry et al. 2017; Schaebs et al. 2017) (Fig. 6.1a, b, and c). While we have not yet quantified our observations that male white-faced capuchins experience an enhancement of their secondary sexual characteristics after attaining alpha status, Fragaszy et al. (2016) recently documented a 20% increase in body mass in male bearded capuchins (*Sapajus libidinosus*) that changed from subordinate to alpha status. The process, they argue, is similar to the rank-dependent weight gain in mandrills (*Mandrillus sphinx*; Setchell and Dixson 2001). In both of these species, weight gain is thought to be triggered by changes in baseline testosterone levels associated with a male's rise to alpha status (Setchell et al. 2008; Mendonça-Furtado et al. 2014), a phenomenon we suspect is also responsible for the changes we have observed in alpha male white-faced capuchins (see Sect. 6.3.4 below; Jack et al. 2014).

6.3.2 Behaving Like an Alpha Male

Within their groups, alpha males are unquestionably the centre of attention, often receiving significantly higher rates of grooming and contact time with other group members compared to subordinate males (Jack 2003). Alpha males (and alpha females) are most frequently found in the centre of their group, though during travel they tend to be in the most forward position (Hall and Fedigan 1997). Being at the front during group movement likely facilitates their priority of access to fruit trees and water since dominance rank has been directly linked to increased energy intake in this species, even in the absence of overt aggression (Vogel 2005).

This forward position in the group may also confer alpha males with the best location for detecting predators or extragroup individuals. Male and female capuchins both engage in vigilance behaviour; however males are more vigilant than females, and alpha males are significantly more vigilant than all other group members (Rose and Fedigan 1995; Perry 1996; Gould et al. 1997; Jack 2001). While some of this vigilance is directed at detecting and avoiding predators, much of it appears to be aimed at detecting conspecifics who might be attempting to take over their alpha position within the group (vigilance is highest in areas of home range overlap where intergroup encounters are most likely to occur) (Rose and Fedigan 1995). Although intragroup relationships among coresident males are tolerant and sometimes affiliative (Jack 2003; Schoof and Jack 2014), severe and sometimes lethal male-male agonism occurs in the context of intergroup interactions and alpha male replacements (Perry 1996; Fedigan and Jack 2004). During intergroup interactions, male white-faced capuchins are the primary participants with alpha males being the first to initiate the encounter and take the lead in the attack, while females only rarely participate and generally flee with immature group members (Jack unpublished data; Perry 1996; Rose and Fedigan 1995; but see Crofoot 2007).

6.3.3 Becoming an Alpha Male

Subadult and juvenile males can quite easily join existing breeding groups as subordinates, often remaining behind with the new group following intergroup interactions or by tagging along with adult males moving between groups (Jack and Fedigan 2004a, b; Jack et al. 2012). However, once males attain adult body size at around 10 years of age, their movement between groups is no longer tolerated, and they must usually fight their way into a bisexual group whether they are attempting to enter as an alpha or a subordinate. To combat this resistance, males often join groups in parallel (dispersing in the company of other males or targeting groups containing familiar males) (Jack and Fedigan 2004a; Perry 2012; see Wikberg et al., 2018, this volume). In cases where multiple males take up residency together, one of them will rise to the position of resident alpha male, often (but not always) with some jockeying among them for this position. We have also observed subordinates dispersing with their group's alpha and continuing to retain their subordinate status through multiple dispersal events.

We have observed male white-faced capuchins to become alpha via all five of the various modes to alpha outlined by Teichroeb and Jack (2017). They are listed here from most to least commonly observed in our study population as reported in Brasington et al. (2017):

1. *Group takeovers*, which usually involve coalitions of extragroup males aggressively attacking and overthrowing the alpha male of a group (33% of AMRs).
2. *Successions*, where a subordinate group male is able to take up the position of alpha male following the death, dispersal, or disappearance of the former alpha male (29% of AMRs). Note that in this case, the departure of the former alpha is not due to aggression received from other males in the group.
3. *Waltz-ins*, where an extragroup male(s) is able to take up residency in a group that is devoid of resident males (often due to their immigration into other groups) (24% of AMRs).
4. *Rank reversals*, where one or more subordinate resident males aggressively challenge and overthrow the existing alpha male and take up this position in the group (10% of AMRs). In both takeovers and rank reversals, the deposed alpha may be killed, remain in the group as a subordinate, or disperse/disappear.
5. *Group fissions*, where an existing group splits into two or more sister groups, with the former alpha retaining his position in one of the subgroups and a subordinate resident male becoming alpha in the other (5% of AMRs).

6.3.4 The Physiology of Alpha Males

Even in the complete absence of observations of how alpha males look and behave, we can discriminate alpha males from subordinate males simply by examining their hormone profiles. Androgens, a group of hormones associated with male secondary sexual characteristics, sexual activity, and aggressive behaviour, have been among the most widely studied hormones with respect to male dominance in mammals. Androgens are associated with the facilitation of aggression in a reproductive context, including aggression that occurs during challenges for access to mates or territory and during the formation of dominance relationships (Wingfield et al. 1990). Therefore, it is not surprising that dominant males in many non-human primate species have higher androgen levels than subordinates when male-male competition is high, such as during the mating season (Bales et al. 2005; Gould and Ziegler 2007), during periods of social instability (Sapolsky 1993; Marshall and Hohmann 2005), or when the timing of challenges for mates or the threat of infanticide is unpredictable (Muller and Wrangham 2004b; Muehlenbein et al. 2004; Beehner et al. 2006; Setchell et al. 2008; Schoof and Jack 2013).

Our cross-sectional analysis found that alpha male fecal androgen (fA) levels in white-faced capuchins were an average of 11 times higher than those of subordinate adult males, whose levels did not differ significantly from subadult males (Jack et al. 2014). A recent longitudinal study of this same species at Lomas Barbudal confirmed these differences (Schaebs et al. 2017). In adult males, elevated fA levels appear to occur independent of male age and be dependent upon attaining alpha status. Schoof et al. (2012) documented a single case of a subordinate male's succession to alpha following the emigration of the group's former alpha male. It took nearly 3 months for this beta male's fA to reach alpha levels. Schaebs et al. (2017) similarly documented increases in fA levels for 15 of the 18 males in their study who rose from subordinate to alpha status. Of the three males who did not experience an increase in fA levels on attaining alpha status, the authors suggest that in one case sampling was an issue (too few samples), while the other two males displayed high androgen levels prior to attaining alpha status due to high levels of competition even as subordinates. Collectively these results indicate that male fA levels may be highly influenced by the competitive situation faced in their groups (Schoof and Jack 2013; Schaebs et al. 2017). Indeed, both of these studies have documented that while fA levels can vary widely across alpha males, within groups, alphas always exhibit the highest fA levels.

Alpha and subordinate male capuchins also differ in the fecal glucocorticoid levels (fGCs), with alpha males generally displaying higher fGCs than subordinate males (Schoof et al. 2012; Jack et al. 2014). GCs are a group of hormones associated with the stress response, which is adaptive in the short term because it focuses energetic resources to areas relevant to immediate survival needs (e.g. energy release) and temporarily suppresses nonvital functions (e.g. growth, reproduction) (Sapolsky 2005). However, long-term or chronic expression of the stress response can be detrimental to individual health (reviewed in Sapolsky 2005; Gesquiere et al. 2011). The relationship between GCs and dominance rank is variable across species and appears to be closely associated with perceived stress by dominant and subordinate individuals (Abbott et al. 2003; Goymann and Wingfield 2004; Sapolsky 2005). For example, in species where threats to male dominance rank are unpredictable, alpha male GC levels will remain elevated (Schoof and Jack 2013), while in other species alpha GCs are only elevated during periods of group instability (Sapolsky 2005).

The higher fGCs in alpha versus subordinate male white-faced capuchins is likely the result of the higher metabolic costs associated with their elevated vigilance and more intensive participation in intergroup encounters and group protection, behaviours which are also undoubtedly influenced by alpha male androgen levels (Schoof and Jack 2013). Given that alpha male capuchins sire the majority of group infants (see Sect. 6.3.5 below), their elevated fGCs are consistent with the idea of perceived risk (Brockman et al. 2009; Schoof and Jack 2013). If their group is targeted for a takeover, alpha males have the most to lose in terms of current reproductive success (i.e. living infants) and future reproductive opportunities, so they should display the highest stress levels. These external threats to male rank are persistent and unpredictable and should lead to consistently higher GC levels in dominant males, as has been reported for chimpanzees (Muller and Wrangham 2004a). However, alpha male GC levels are undoubtedly influenced by other social factors such as the number of coresident males, dependent infants, and/or fertile females in the group (Schoof et al. 2012, 2016; Schoof and Jack 2013). GC levels are also impacted by environmental factors such as rainfall, temperature, or photoperiod (Schoof et al. 2016).

6.3.5 Reproducing Like an Alpha Male

The behavioural, physical, and physiological alpha male traits described above do not come without costs. High-ranked males may experience higher energetic costs (Barrett et al. 2003; Muller and Wrangham 2004b; Muehlenbein et al. 2004; Gesquiere et al. 2011; Mendonça-Furtado et al. 2014), increased rates of injury (Rose 1994; Rose and Fedigan 1995; Drews 1996; but see Archie et al. 2012), and greater health risks (Sapolsky 1993; Muehlenbein 2009; Muehlenbein and Watts 2010; but see Archie et al. 2012). However, in capuchins, as in many other primate species, this assemblage of alpha male traits collectively enables certain males to successfully compete with other males to gain access to breeding groups of females, the benefits of which can be enormous (Di Fiore 2003). This is certainly the case for alpha male white-faced capuchins as they sire between 70 and 100% of all offspring born during their tenure (see Chap. 7 by Wikberg et al. 2018, this volume; Jack and Fedigan 2006; Muniz et al. 2010; Perry 2012).

While the discovery of high reproductive skew towards alpha males can be explained as benefits for the high costs associated with occupying this position, these results were nonetheless curious given the behaviour of subordinate adult male group members. Subordinate adult males are fully integrated into their social group rather than occupying a more peripheral position, as has been reported for some populations of the closely related tufted capuchins (e.g. Janson 1986). For example, subordinate adult male white-faced capuchins also engage in affiliative behaviours with adult females, males, and immature group members (Jack 2003; Schoof and Jack 2014), and, while their vigilance efforts are not at the level of alpha males, they play a key role in group defence from both predators and extragroup males (Rose 1994; Rose and Fedigan 1995; Jack 2001). Because the presence and activities of subordinate males provide benefits, alpha males make a concerted effort to keep them in the group. When subordinate males are separated from the group, alphas will repeatedly lost-call (capuchin long calls) for them, and, once reunited with the group, alphas perform an elaborate reunion display similar to that observed during mating (see description in Perry 1998a). It is also not surprising then that alphas are tolerant of the mating activities of subordinate males and overt intragroup male-male mating competition is rare (Schoof et al. 2014b). While our evidence to date indicates that a female is more likely to mate with a subordinate adult male when she is pregnant or lactating (Carnegie et al. 2005), some subordinates do sire offspring, particularly when alpha males have long tenures and their daughters begin to reproduce (Muniz et al. 2006, 2010; Godoy et al. 2016a, b; Wikberg et al. 2017 and Chap. 7 in this volume).

6.4 Alpha Males as Keystone Individuals: The Impact of Alphas on Group Success and Survival

It is clear from the above review that alpha males embody a distinct category of individual and occupy a unique role within capuchin groups. However, according to Modlmeier et al. (2014), it is critical to differentiate keystone individuals from "generics" the latter of which they argue are replaceable. One could argue that an alpha male capuchin is replaceable in that when he is gone, another male quickly takes up the vacant position in the group and rises to alpha status (e.g. Perry 1998b; Schoof et al. 2012). It is not, however, that simple. The removal of a true keystone individual should differ from the removal of a generic in that the former should have lasting consequences to the group (Modlmeier et al. 2014). To differentiate between the two, therefore, requires removal experiments (Sih et al. 2009) and comparisons between the effects of removing keystone individuals and other, generic, individuals.

All male white-faced capuchins disperse from the natal group at approximately 4 years of age (Jack et al. 2012), and males continue to move between groups throughout their lives at approximately 4-year intervals (Jack and Fedigan 2004a). This pattern of dispersal means that most males reside in three or more distinct social groups during their lifetimes, occupying varying ranks, and some males are alphas in more than one group (Jack and Fedigan 2004a; Schaebs et al. 2017). This regular occurrence of adult male dispersal, and the frequent turnover of group alpha males (alpha male replacements), provides natural removal experiments enabling the examination of their consequences on group dynamics.

The removal (i.e. death, disappearance, dispersal) of any individual from a social group will have some sort of measurable impact on a group. For example, we have documented the impact of subordinate male dispersal on the vigilance behaviour of alpha males (Jack 2001). Here we examine the impacts of male movement on group demographics via an examination of infant mortality in association with changes in male group membership. Increased infant mortality in association with changes in a group's alpha male has been well documented in primates and other social mammals, particularly for those in which male dominance rank is positively associated with male reproductive success (see review by Palombit 2015). In our study groups, we have shown that infant mortality increases significantly during times associated with alpha male replacements compared with periods of stability in the male dominance hierarchy (e.g. Fedigan 1993; Fedigan et al. 2008; Kalbitzer et al. 2017; Brasington et al. 2017). However, we have not yet examined the effects of subordinate adult male dispersal on infant mortality (nor are we aware of these data for other species), a comparison critical to determining whether white-faced capuchin alpha males are indeed true keystone individuals. Following Modlmeier et al. (2014), we address this issue by exploring the following questions:

1. What impact does the "removal" of an alpha male have on infant mortality?
2. What impact does the "removal" of a subordinate adult male have on infant mortality?
3. Are the effects of alpha male replacements (AMRs) on infant mortality long-lasting?

We examined long-term data on infant births and deaths, as well as data on male movement and rank change in five study groups for variable periods between 1986 and 2015 (a total of 85 group years; see Fedigan and Jack 2012 for additional details on data collection). During this period, we documented the birth of 221 infants, 21 alpha male replacements, and the emigration of 53 subordinate adult non-natal males (i.e. all immigrant males aged 10 years and older). Our analysis is restricted to adult males because (a) in all but very rare circumstances (i.e. where there are no other males in the group), only adult males become alphas, (b) we have never observed or suspected a non-adult male to kill an infant, and (c) subadult males only rarely sire offspring (unpublished data; see also Muniz et al. 2010). Based on our prior observation that infants (<1 year of age) are more vulnerable to infanticide in association with alpha male replacements (Fedigan 2003) and following Brasington et al. (2017) and Kalbitzer et al. (2017), we divided our sample of 221 infants into (a) those born in association with an AMR in that the infant was <1 year at the time of the AMR, or was born within 5.5 months following the AMR (i.e. sired prior to but born after the AMR; 5.5 months is the median gestation length for *C. c. imitator*, Carnegie et al. 2011), and (b) those born during periods of group stability.

6.4.1 What Impact Does the "Removal" of an Alpha Male Have on Infant Mortality?

In our most recent analysis (Brasington et al. 2017), we documented infant mortality in association with AMRs at 50.9%, a mortality rate more than double the 26.2% recorded during times of group stability (Fig. 6.2) (see Perry 2012 for similar findings in the Lomas Barbudal capuchin population). As mentioned above, all five types of AMRs have been observed in the Santa Rosa capuchins, and each is associated with observed infanticides and higher mortality rates than recorded during periods of group stability (Brasington et al. 2017). Only 4 of the 21 AMRs in our sample were not associated with infant deaths; 2 of these involved groups that did not contain infants, the third involved a group that contained a single infant aged 7 months, and the fourth involved a group that contained a single infant aged 10 months, which puts them at a significantly lower risk of infanticide than infants <6 months of age (Brasington et al. 2017).

Over the years of our study in Santa Rosa, we have witnessed many infanticides and have strong inferential evidence that many more "missing infants" have been the victim of infanticide. While a few cases of infanticide have occurred during periods of social stability (Schoof et al. 2014a), the majority occur during periods associated with alpha male replacements. AMRs are often, but not always, associated with high levels of aggression exchanged between resident and incoming males. However, infant deaths and disappearances most often occur after a new alpha male has established himself in the group, rather than during the initial periods of aggression associated with AMRs (Brasington et al. 2017). In many cases, infants that are born up to 5.5 months after an AMR are targeted, and these infants, who were confirmed or strongly suspected as offspring of the former alpha male, experience the highest observed mortality rates in our sample (63%; Brasington et al. 2017).

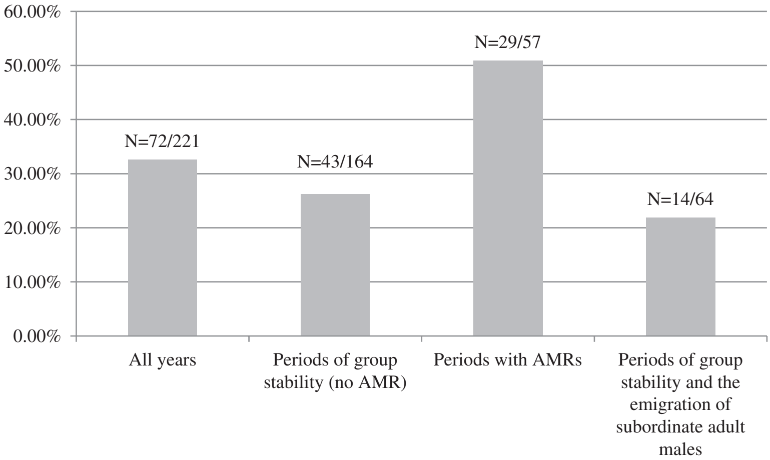

Fig. 6.2 Infant mortality rates across all years and in association with periods of group stability, alpha male replacements, and subordinate male emigrations (N = # of infants died/total number infants born during each period)

6.4.2 *What Impact Does the "Removal" of a Subordinate Adult Male Have on Infant Mortality?*

When a subordinate adult male dies or disappears, he is not "replaced by another male". Indeed, many of our study groups have spent long periods of time with the "alpha" as the sole resident male following the dispersal of all subordinate males (e.g. Jack 2001, 2003; Jack and Fedigan 2004b). A total of 53 subordinate, non-natal, adult males emigrated or disappeared (referred to as emigrations from herein) from our groups during the study period. Of these males, 22 emigrated in association with AMRs, in that their emigration coincided with the departure of the former alpha male and often other adult and immature males in the group. As mentioned above, male white-faced capuchins often engage in parallel dispersal, and during AMRs it is not uncommon for all males to emigrate simultaneously, resulting in a complete replacement of resident group males (Fedigan and Jack 2004; Jack and Fedigan 2004a; Wikberg et al. 2014). The 22 males that emigrated in association with an AMR were not included in these analyses due to the confounding impact of AMRs on infant mortality.

The remaining 31 subordinate males in the sample emigrated during periods of stability in the group's alpha male. Following the same criteria used above for alpha male removals, 64 of the 164 infants born during periods of group stability were either <1 year at the time of the subordinate male emigration or they were born within 5.5 months following the emigration event (i.e. sired prior to but born after the emigration). Of these 64 infants, 14 died before reaching 1 year of age, for a mortality rate of 21.9% (Fig. 6.1). This is lower than the infant mortality rate recorded during periods of group stability (26.2%) and less than half of the 50.9% infant mortality rate recorded in association with AMRs.

While these results demonstrate that the removal of an alpha male has a much greater impact on infant mortality than does the removal of a subordinate adult male, it is important to note that the removal of subordinates is not without consequence to other group members. Capuchin groups lacking subordinate adult males are less able to win intergroup competition for resources, such as access to water or fruit trees (Crofoot et al. 2008; Perry 1996; Rose and Fedigan 1995), and they are at greater risk of alpha male replacements than are groups with multiple resident adult males (Fedigan and Jack 2011). In addition, in the current data set, there were several instances in which the death/disappearance of infants appeared to be directly related to the departure of the subordinate; 5 of the 14 infants in our sample that died/disappeared in association with a subordinate male leaving the group occurred in close temporal association with the subordinate male's emigration, and 1 of these deaths was an observed infanticide by the group's alpha. The differentiating feature here, however, is that the resulting infant death was due to the action of the resident alpha male, rather than a new male taking up the subordinate's position, as we have documented to occur in the wake of AMRs. Unfortunately, this observation was made in the early years of our study (the 1980s) predating our routine use of genetic paternity data; thus we are not able to determine if the infant killed by the alpha male was sired by the departed subordinate male.

6.4.3 Are the Effects of Alpha Male Removals on Infant Mortality Long-Lasting?

In their conceptual framework, Modlmeier et al. (2014) stress the importance of determining if the removal of keystone individuals has long-lasting effects or if they end after a new individual takes up that particular role or position in the group. Sapolsky and Share (2004), for example, documented the long-lasting effects of the death of all high-ranking aggressive males in a troop of olive baboons (*Papio anubis*) after a tuberculosis outbreak in their study group. Following their "removal" the remaining, more passive, group males rose to the higher ranks, and the entire temperament of the group became more docile in nature, and these changes persisted for more than a decade.

In white-faced capuchins, the impacts of AMRs are very long-lasting. AMRs occur over a period of weeks or months, while the new male(s) integrate themselves into the group, sometimes jockeying for the alpha position when more than one male immigrates together. In addition, female and immature members of the group will flee from and avoid these new males, and it can take many weeks before they begin to tolerate their presence and accept them into the group (Fedigan and Jack 2013). Prolonged female avoidance of these new males is likely a counterstrategy to infanticide, which occurs not only in the immediate context of the replacement itself but continues well after the new alpha male is established in the group. Of the six observed or strongly inferred infanticides in our sample (dead infants were found with canine puncture wounds similar to those in observed cases), the range of time from AMR to infant death was 0–90 days (mean = 46 days). If we extend this to our entire sample of infants that perished in association with AMRs, the mean time between the AMR and infant death was 98 days (range 0–254 days, median 94 days), including numerous cases where infants born up to 5 months following an AMR have perished. These latter infants would have most likely been sired by the group's previous alpha male (median gestation length is 5.5 months; Carnegie et al. 2011). Thus, the impact of alpha male removal on infant survival can last for many months. The impact on female reproduction is even longer lasting. If, for example, a female loses a 3-month-old infant, this represents a minimum of 20.5 months of reproductive time lost (5.5-month gestation +3 months of rearing lost infant +6.5 months post-nursing infertility period [Recabarren et al. 2000] + 5.5-month gestation for the next infant). If a female is very successful and experiences, for example, a 15-year reproductive career, the death of this 3-month-old infant in association with a single AMR represents 11.4% of her reproductive career. It is little wonder that female capuchins actively promote multi-male groups and resist AMRs to the best of their abilities (Fedigan et al. 2008; Fedigan and Jack 2013).

6.5 Discussion

In light of the evidence presented here, white-faced capuchin alpha males appear to be keystone individuals; they have a large impact on group dynamics and success relative to their representation in the population, and their "removal" from a group has a much larger, and long-lasting, impact on group dynamics (infant mortality in particular) than does the removal of a subordinate male. To be sure, changes in alpha males within groups are associated with a suite of consequences extending well beyond increased infant mortality. The demographic impacts of AMRs can continue for years and may indefinitely influence the lives of some individuals. As we have shown elsewhere, changeovers in a group's alpha male impact female reproductive success by altering interbirth intervals (Fedigan et al. 2008), and they can even disrupt the species-specific pattern of female philopatry (Jack and Fedigan 2009). Infants and juveniles that survive an AMR may be nonetheless impacted by the availability (or lack thereof) of play, alliance, and dispersal partners (e.g. see Perry 2012). Infant mortality in association with AMRs will impact the presence of kin in the social group, which may be of particular importance in species where male coalitions are a prime determinant for battles over rank acquisition and maintenance (Bissonnette et al. 2015). In species like white-faced capuchins, long-term coalition partners, who may or may not be kin, are maintained via parallel dispersal that persists even into adulthood (Jack and Fedigan 2004a, b; Perry 2012; Wikberg et al. 2014). These partners can impact a male's success in entering a social group, rise to alpha status, and, ultimately, reproductive success.

Given that alpha males sire the majority of offspring born into a group, AMRs often result in the removal of the father of surviving infants and juveniles. Studies from several primate species have now shown that the presence of the father in the group during immaturity can impact the timing of a number of key life-history events. For example, Charpentier et al. (2008) found that offspring age at sexual maturity decreased for both male and female baboons when the father was present in the group. Perry et al. (2017) have shown that in white-faced capuchins, the occurrence of AMRs during the first 5 years of a male's life influences the timing of natal dispersal and an individual's rise to alpha status.

It is clear that the "removal" of an alpha male from a group has far-reaching, long-lasting impacts. While our discussion has focused on the impact of the "natural removal" of an alpha male (via death, predation, dispersal, or group takeovers), the same impacts will be felt following the "unnatural removal" of an alpha male, such as occurs from poaching. While Costa Rica is well-known for its progressive conservation initiatives (Kappelle et al. 2016), poaching remains an ongoing threat to wildlife. When a capuchin group encounters a poacher, it is the alpha male who takes the lead in defending the group. He will threaten the poacher, often for an extended period of time and at relatively close range, while the rest of the group retreats into the forest. Similar observations have been made where alpha males will threaten oncoming traffic (such as a busload of tourists) while the group crosses the tarmac. The death of an alpha male, no matter whether from poachers or an oncoming vehicle, sets off a chain of events. A new male will quickly try to take up the alpha male position in the group, most likely fighting (sometimes to the death) with other males who also want to assume the alpha position. Group infants will die, adult females will be injured trying to protect their infants, and group demographics will be altered, the impacts of which will remain for years or even lifetimes (e.g. the availability of coalitionary and dispersal partners and the timing of important life-history events). Knowing that killing an alpha male is not simply killing a single monkey, but that these actions will negatively impact that entire group and possibly the community, may help inform community-driven conservation initiatives (e.g. see Jiménez et al. 2017).

While it is clear alpha males play a unique role in group dynamics and success, we are still far from understanding the mechanisms underlying how and why some males become alphas and others do not. Do all males have the capacity to become an alpha male, or is there only a certain "type" of male who is able to attain alpha status? Modlmeier et al. (2014, pp 58–59) suggest that the emergence of keystone individuals occurs (1) via Darwinian selection for their particular "keystone-conferring genotype" and/or (2) due to particular "experiential, state-dependent, or context-dependent phenomenon". We have documented a suite of both behavioural and physiological characteristics associated with alpha male white-faced capuchin, some of which are likely to be under genetic control or influence. Given the strong genetic determination of testosterone levels identified in humans (Ohlsson et al. 2011), it is likely white-faced capuchins are similar in that only some males have the potential to produce the extremely elevated androgen levels characteristic of alpha males (Schoof et al. 2012; Fragaszy et al. 2016; Schaebs et al. 2017) and the immune system to sustain chronically elevated cortisol levels (Sapolsky 2005; Rakotoniaina et al. 2017; but see Beehner and Bergman 2017). If there is a heritable component to an individual's ability to attain high dominance status (e.g. the ability to produce high levels of androgens), it is equally likely that a specific set of environmental variables need to align to enable a particular male to realize this potential. These environmental variables may include (but are not limited to) maternal androgen levels during prenatal development (e.g. Ryckmans et al. 2015), maternal rank (e.g. Meikle and Vessey 1988; Onyango et al. 2008; Surbeck et al. 2011), access to sufficient nutrition during key developmental phases (e.g. Lee et al. 2013), the presence of the father in a group during development (e.g. Lynch et al. 2017), the timing of pubertal onset (e.g. Bercovitch 1993), and/or the possession of particular social skills or personality types that may be acquired or informed during socialization (e.g. Perry et al. 2017).

It is important to remember that dominance is a social construct dependent upon the interactions and reactions of given individuals in particular situations. It is likely that some male capuchins who possess the potential to display the suite of alpha male traits never have the opportunity to become an alpha male. Likewise, it is possible that some males who do not possess these traits will nonetheless be able to take up the role of alpha male within a group as a result of particular circumstances (e.g. being in the right place at the right time). For example, Perry and Manson (2008) describe a situation where multiple adult males fought for the alpha position over several years. Eventually all of these males were so badly wounded that they deserted the group, opening up the opportunity for young, inexperienced males from a neighbouring group to “waltz-in” and take up residency uncontested. We have observed similar cases in our own study groups in Santa Rosa. In one of our smallest study groups, a subadult male (aged 8 years) rose uncontested to alpha status after the group’s alpha disappeared following an intergroup encounter. The young male remained alpha for almost 3 years and sired three infants, though none survived their first year of life despite being born during a period of group stability (i.e. their deaths were not associated with AMRs). We have also observed two cases where a series of botched takeover attempts eventually lead to the extinction of the groups, with group females disappearing or emigrating to neighbouring groups (Jack and Fedigan 2009).

6.6 Conclusions and Future Directions

Identifying traits and processes influencing individual variability in reproductive success is fundamental to understanding evolutionary processes. In white-faced capuchins, as in many other socially living mammals including humans, one of the key variables influencing male reproductive success is dominance status (Jack and Fedigan 2006; Muniz et al. 2010). However, we still know very little about how and why some males attain alpha status while others do not. Indeed few studies conducted to date have investigated differences in males prior to their achievement of a particular rank in a dominance hierarchy (see Bercovitch 1993; Setchell and Dixson 2001; Beehner et al. 2006; Schoof et al. 2012; Schaebs et al. 2017). Such data are crucial to furthering our understanding of how dominance impacts the behaviour and reproductive success of individuals and his/her surrounding conspecifics (Chichinadze et al. 2014).

The majority of research on keystone individuals conducted to date has focused on how the addition or removal of keystone individuals displaying particular behavioural types impacts collective behaviour and group success within groups of social insects (e.g. Sih and Watters 2005; Pruitt and Pinter-Wollman 2015; Pinter-Wollman et al. 2017). Due to the constraints on a primatologist’s ability to experimentally manipulate group composition, this line of research remains virtually unexplored in wild primates. What little is known does not address the keystone individual concept directly and remains largely descriptive. However, as was the case in the current study, the natural dispersal of keystone individuals from the group enables researchers engaged in long-term behavioural studies to document the resultant effects of the departure of such individuals.

The analysis of primate personalities may provide another arena for exploring and identifying the traits and emergence of keystone individuals. Perry et al. (2017) recently examined the effects of personality types on the age of natal dispersal and the time to attaining an alpha male position in wild white-faced capuchins. They found that more extraverted males (those that were scored as more social, aggressive, assertive, fearless, etc.) attained alpha status sooner than males displaying other personality types. This area of research, and the ongoing long-term studies of wild primates across taxa (see Kappeler et al. 2012), holds promise for future analysis of how keystone individuals longitudinally impact group success. It is time, as Modlmeier et al. (2014, p. 53) suggest, for us to pay more attention to the consequences of trait variation at the individual level, rather than continuing to ignore it and treat it as "*mere statistical noise*".

The study of keystone individuals and their impacts on social groups, populations, and communities is still in its infancy, and we are just beginning to recognize the evolutionary, ecological, and conservation importance of these individuals (Modlmeier et al. 2014). Future research on this topic, particularly in long-lived species such as primates, should explore variation in trait expression across keystone individuals, as well as the impacts of this variation on both individual and group success, and examine the social and ecological factors influencing the development and manifestation of these traits. Further exploration of whether or not alpha individuals, both males and females, in other species may fit the definition of keystone individuals is also warranted.

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