Impact of personality traits and early life experience on timing of emigration and rise to alpha male status for wild male white-faced capuchin monkeys (*Cebus capucinus*) at Lomas Barbudal Biological Reserve, Costa Rica

Short title: Early careers of male white-faced capuchin monkeys

Authors:

Susan Perry[1,2,4], Irene Godoy[1,2,4], Wiebke Lammers[3,4], & Andy Lin[5]

[1]Dept. of Anthropology, University of California-Los Angeles, 375 Portola Plaza, Los Angeles, CA 90095-1553, USA

[2]Behavior, Evolution and Culture Program, University of California-Los Angeles, 375 Portola Plaza, Los Angeles, CA 90095, USA

[3]College of Life and Environmental Sciences, University of Exeter, Penryn Campus, Cornwall TR10 9FE UK

[4]Proyecto de Monos, Apdo 5, Bagaces, GTE, Costa Rica

[5]Statistical Consulting Group, Institute for Digital Research and Education, University of California-Los Angeles, 375 Portola Plaza, Los Angeles, CA 90095, USA

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Summary:

It is rare in studies of long-lived animals to know enough about the personalities and early experiences of individuals to use this information to predict their behavior during major life transitions in adolescence and adulthood. Here, we examine how personality traits and early experiences predict age of natal emigration and timing of first ascent to alpha status in 169 wild male white-faced capuchins studied at Lomas Barbudal, Costa Rica, 75 of whom emigrated and 23 of whom acquired alpha status. Males were more likely to delay natal emigration if they were more extraverted, more neurotic, if their fathers co-resided longer with them, and if there were fewer alpha male turnovers. More extraverted males attained alpha status sooner.

Keywords: Male life histories, personality, dispersal, dominance rank, capuchins

Introduction:

A thorough explication of the factors that impact male lifetime reproductive success necessitates investigation of males' early development and intrinsic characteristics, and the timing of important life history events that affect the onset of reproduction (van Noordwijk & van Schaik, 2001; Alberts, 2012). Although it is generally recognized that many important events in the life histories of individual animals are likely to be influenced by both personality -- i.e. those characteristics that describe and account for stable individual differences in behavior -- and experiences during

early development (Dingemanse et al., 2002), it is rarely possible to document these relationships in the wild, particularly for long-lived animals like primates. This is particularly true for species in which males disperse (i.e. most mammalian species (Dobson, 1982; Cockburn, 1992; Wolff, 1993; Alberts, 2012)), because it is hard to track males once they have left their natal groups.

Although the relationship between male dominance rank and reproductive success (RS) is variable both within and between species, dominance rank is usually an important determinant of breeding success in mammals, including primates (Cowlishaw & Dunbar, 1991; de Ruiter & van Hooff, 1993; Ellis, 1995; Alberts, 2012), and this is particularly true in white-faced capuchins, *Cebus capucinus* (Muniz et al., 2010). Because rank is so important for attaining RS, understanding the determinants of lifetime RS requires an understanding of how males rise to alpha status.

In this study of wild white-faced capuchin males, we investigate the relationship between two personality traits (extraversion and neuroticism) and the timing of two important life history events: natal emigration and first rise to alpha status. We also investigate the relationships between these outcomes and two forms of early experience: frequency of social play and social stability (as measured by co-residence of the young male with his father and by the number of alpha male turnovers during the male's juvenile phase).

Age at natal emigration, and age at first rise to alpha status, are expected to be fitness-relevant outcomes because (a) most breeding is accomplished by alpha males (Muniz et al., 2010), and (b) males typically first achieve alpha status after

emigrating,. In white-faced capuchins, females are philopatric and males disperse (Perry, 2012). Reproductive skew is high in this species, with alpha males essentially monopolizing breeding opportunities with females who are not their direct descendants (Muniz et al., 2006; Muniz et al., 2010; Godoy et al., 2016).

The ubiquity of coalitional aggression among capuchins (Perry, 2012) implies that achieving and maintaining alpha status generally requires both fighting skills and advanced social skills. The latter enable individuals to manage relationships with allies who are necessary for helping a male attain alpha status and defend his reproductive access to females from rival males (Perry 2012, Perry and Manson 2008). Social play has been hypothesized to hone fighting skills and also social negotiation skills (Bekoff, 1988; Byers & Walker, 1995; Bell et al., 2010; Pellis et al., 2010). Thus, we predicted that males who spend more time engaged in rough-and-tumble play as juveniles will be capable of achieving an alpha male position more quickly upon entering a new group, compared to males with less play experience.

The form of early life experience that seems most likely to affect males' decision-making about how long to remain in their natal group is the stability of the alpha male position. Alpha male turnovers are bloody, chaotic events that typically result in high rates of infanticide as well as wounding or even death of other group members (Fedigan, 2003; Perry & Manson, 2008; Perry, 2012; Perry et al., 2012). Past research at Lomas revealed that 24% of takeovers were accomplished by groups of co-migrant males invading from the outside, and 61% were internal takeovers by long-term resident males (Perry et al 2011); in all of these cases, the

takeover involved violent conflict between the old alpha male and his challenger(s). Sometimes the takeover is rapid, taking only a single day, and other times there is a phase of repeated challenges and reversals lasting for a few months. In a few cases, the alpha male acquired the position peacefully, when the former alpha male died of extrinsic causes or migrating males chanced upon a new fission product that did not yet have males attached to it. In all cases except for peaceful inheritance by a resident, infanticide was a common outcome. Previous work on the timing of natal dispersal in white-faced capuchins at the nearby site of Santa Rosa has found that natal dispersal is far more likely during the social instability period characterizing the aftermath of an alpha male takeover (Jack et al., 2011).

Intrinsic factors such as personality, health or body size may affect the types of strategic options available (Sapolsky, 1991), influencing decisions about the timing of investment in somatic vs. reproductive effort, and the tradeoffs between survival and reproduction. A recent meta-analysis of personality traits that encompassed both vertebrates and invertebrates found that bolder males, i.e. those willing to take more risks, had higher short term reproductive success but lower survival (Smith & Blumstein, 2008). Personality traits, or behavioral syndromes (Sih et al., 2004), may be adaptive in some circumstances but not others, and furthermore, individuals may lack the capacity to adjust their behavior so as to apply it only in the circumstances in which it is most favorable. For example, in Namibian rock agamas, bold males are more exploratory (which gives them access to more food resources) but also are excessively bold in approaching predators, which is probably responsible for their higher rates of tail loss (Carter et al., 2010).

Very little research on the fitness correlates of personality traits is available from nonhuman primates. However, various personality traits ("niceness," "aloofness" and "loner") in baboons influence their degree of sociality and capacity to form stable long-term relationships (Seyfarth et al., 2012), which in turn probably influence their fitness (Silk et al., 2009; Silk et al., 2010).

Research on our study population (Manson & Perry, 2013) has revealed a personality structure comprising five dimensions. One of these, Extraversion (see methods section on personality ratings for definition of Extraversion and Neuroticism), encompasses three facets of human Extraversion (Costa & McCrae, 1995): Gregariousness, Assertiveness, and Excitement Seeking. We predicted that more extraverted males would emigrate earlier and also become alpha males earlier, as these attributes would make them more confident and persistent in challenging dominants and in establishing new relationships outside their natal groups.

A second personality dimension in *C. capucinus* is Neuroticism (Manson & Perry, 2013), which encompasses the Anxiety, Angry Hostility, and Impulsivity facets (Costa & McCrae, 1995) of human Neuroticism. High levels of Neuroticism might be expected to impair capuchin males' ability to develop the physical competitive ability and social skills necessary to successfully emigrate and form the alliances necessary to acquire and maintain a breeding position. We base this prediction on findings that highly neurotic humans are more prone to psychiatric disorders and chronic somatic ill health (Claridge & Davis, 2001; Neeleman et al., 2002), and also on findings that neuroticism predicts social isolation and marital

relationship failure in humans (Kelly & Conley, 1987). On the other hand, the increased impulsivity of neurotic capuchins might lead them to attempt emigration or challenge alpha males sooner than less neurotic males might (though these attempts would be successful only if the male were physically and socially prepared to compete successfully in a new situation at that age). The anxiety component of neuroticism might serve a useful adaptive function for capuchins, causing them to monitor their rivals or detect predators more effectively.

It is likely to be the case that emigrating sooner increases the chances of acquiring a breeding position earlier in life (thereby possibly extending his total number of reproductive years), but this is not necessarily the case, depending on both intrinsic characteristics of the male (e.g. current body size, health and age) and the quality of his demographic situation in the natal group in comparison to his dispersal options (e.g. how many males are ahead of him in a reproductive queue, or how many non-kin females are available as potential breeding partners). Males with low competitive ability for their age might, for example, benefit from staying longer in the natal group and/or deferring a competitive push for an alpha male position until their body mass and fighting skills have improved (Heg et al., 2011) . The natal group is likely to be a "safe haven" (Kokko & Ekman, 2002) where males can continue to invest in somatic effort if males' parents or other tolerant close kin remain in the group longer. If the natal home range is of particularly high quality and a natal male stands a good chance of inheriting breeding access to this group, he may do better to delay dispersal rather than to disperse and breed earlier in a group that has a lower quality home range and worse breeding opportunities (Stacey &

Ligon, 1991; Heg et al., 2011). Also, staying longer with kin might afford indirect fitness benefits if there are opportunities to defend the natal group from infanticidal males or provide alloparenting to closely related immatures.

This study aims to answer two questions: (a) what factors impact the age at which males emigrate from their natal groups, and (b) what factors impact the age at which males first become alpha males? Specific predictions follow.

Predicting age of emigration:

We predicted that more extraverted males would leave earlier (being less intimidated by novel social situations and more skilled at forming new relationships). We had no specific directional prediction for neuroticism; although we expected neuroticism to cause monkeys to be less adept at relationship formation, these circumstances might either cause earlier emigration (due to low satisfaction with relationships in the natal group) or later emigration, due to lack of skill in forming new relationships outside the natal group. The impulsivity dimension of neuroticism might promote earlier emigration, whereas the anxiety dimension might promote later emigration. We predicted that males would emigrate sooner if there were frequent alpha male turnovers in their groups during their first five years of life, since such turnovers are associated with higher incidents of wounding of group members (and presumably a more stressful social environment overall). We predicted that males would stay longer in natal groups if their fathers stayed in the group longer. One reason to predict delayed emigration

when fathers remained in the group longer is that longer paternal residence probably means that a potential emigrant had a larger number of younger paternal siblings in the group. Not only would these younger siblings possibly become co-migrants who aid one another later in life, but there might also be indirect fitness benefits derived from contributing to group defense, and thereby promoting the survival of paternal siblings. Another reason to stay is that a father (even a subordinate father) might provide continued protection and coalitionary support to sons even if he were not the alpha male, thereby increasing the benefit:cost ratio of staying longer to invest in somatic effort.

Predicting age of first acquisition of alpha status:

Males face a major social challenge when they first emigrate and seek a position where they could breed. Perhaps for the first time in their lives, they must form alliances and competitive relationships with monkeys who are unfamiliar to them. Their ability to solve these challenges determines whether they succeed in acquiring alpha status and hence an early opportunity to breed. Greater amounts of social experience and fighting skills (as assayed by percentage of time spent engaging in rough-and-tumble play during the first five years of life) were hypothesized to predict earlier success at becoming an alpha male. We also hypothesized that more extraverted males would achieve alpha status earlier, for the following reasons (which we couldn't test directly in a quantitative way): We thought they would be better at forging alliances both with potential allies from the natal group and with

resident males and females in the group to which they disperse, and be more confident about attempting takeovers. We were less certain what to predict about neuroticism, though we suspected it might be relevant: either more neurotic males might be more (productively) vigilant, or their anxiety levels might prevent them from achieving the social competence necessary to become alpha males.

Material and methods:

Study site and subjects:

The data in this study were collected as part of a 25-year study of the behavioral ecology of white-faced capuchins at Lomas Barbudal, Costa Rica and surrounding areas that began in 1990 (see Perry 2012 and Perry et al. 2012 for further details regarding the demography and social dynamics of the Lomas Barbudal population and the history of the study). This study used data collected up through November 2015. The social groups included 10 stable groups including both males and females that were regularly monitored, and five multi-male/multi-female groups that were more sporadically monitored, plus various all-male groups. This dataset includes data from 169 males born into nine social groups. Natal emigration was observed for 75 of these males, and 23 attained alpha status during the study period. Data on personality traits and on father presence or play experience during the juvenile phase were available for subsets of this larger data set.

Past research on *Cebus capucinus*, from the two long-term sites where male life histories and social relationships have been studied (Lomas Barbudal and Santa Rosa), has revealed that this is a female-philopatric species in which males disperse, often with other males who are frequently their kin (Jack & Fedigan, 2004a; Jack & Fedigan, 2004b; Perry, 2012; Wikberg et al., 2014). The mean group size at Lomas is 18.8 (range: 5-40), with adult male:female sex ratios varying from 0.22 to 1.44 (Perry, 2012). Most groups contain multiple adult females and multiple adult males, but one-male groups are sometimes observed (though they eventually attract additional males).

Demographic data:

Whenever monkeys were encountered, researchers noted the identities of all monkeys that were in visual or auditory contact of one another as being in the same social group. Most social groups encountered were composed of relatively stable sets of individuals, but lone monkeys and clusters of co-traveling males were noted also. Census data were collected systematically in this way, on checksheets designed for this purpose, beginning in July 2006 and continuing to the present. Prior to that time, notes about contact with monkeys were kept in field notebooks and also recorded in the behavioral data; these data were later extracted from these sources to create a census database. The number of monkeys and social groups increased over time, and the number of days that each group was followed per month varied as a function of the ratio of on-site researchers to social groups. In general, effort

was made to census each primary research group at least once per month. When there was evidence of social tension among males and hence instability in male dominance ranks, that group was censused more frequently, thereby reducing the possibility of missing rank changes.

Determination of dominance ranks:

Past research on the rank relations and social dynamics of male capuchins (Perry, 1998b; Perry, 1998a) indicates that the best predictors of dominance rank are spontaneous submissive behaviors (avoidance and cowering) in the context of dyadic social interactions. In this species, alpha males are typically readily distinguishable from subordinate males not only by the direction of these submissive behaviors, but also because, compared to subordinates, they generally exhibit far more piloerection, display behaviors, vocalizations and urine-washing, and they occupy more spatially central positions within their group (Perry, 1998b; Perry, 1998a; Campos et al., 2007). Whereas alpha males are normally easy to identify, the rank relations between subordinate males are far murkier and cannot always be readily detected (Perry, 1998b; Schoof & Jack, 2014). There were some cases of alpha male rank reversals occurring during observation gaps, and of course it is possible that there were multiple turnovers in some of these longer gaps. Nonetheless, if there was an observation gap bounded by days in which the same male was alpha male at both ends, we assumed continuity in the alpha male position during that gap, and if there was a different male who was alpha at each end of the

gap, we assumed just one turnover. In cases for which the date of the turnover was not known precisely, we used the average between the earliest and latest possible date as the date of the turnover.

Measurement of play:

The percentage of time that males spent playing during the months 7-60 of their lives was determined by calculating the proportion of scan samples in which the monkey was engaged in rough and tumble play (i.e. play chasing, hitting, wrestling and biting, either quickly or in slow motion). Scan samples were collected either as group scans, for the 43 males whose juvenile periods occurred after January 2001 (average 1460±944 scans/male, range 65-3509), or as instantaneous scans during focal follows for 7 males whose juvenile periods occurred prior to 2001 (average of 75±17 scans/male, range 53-102). During group scans, each monkey's activity was recorded during the first instance in which the monkey was seen, at intervals no closer than 10 minutes. During focal follows in pre-2001 data, instantaneous scans were performed at 2.5-minute intervals. Because there was no clear change in time spent playing between months 6-60, these data were pooled. For the analysis in which play was used to predict age of emigration, the scan data collected post-emigration were dropped from the analysis. No male became alpha male during his first five years of life, and hence none of the scan data used to calculate play experience were from males who had already become alpha.

Personality measures:

In the early days of animal personality research, there was a tendency to rely more on behavior ratings than observer ratings of personality traits in order to characterize individuals' personalities, because of a suspicion that humans' ratings of another species' personalities might introduce anthropomorphic bias. However, a growing body of work in the rapidly expanding field of animal personality research has revealed that human observer ratings of animal personality traits are not only logistically more feasible in a wide range of circumstances, but also (a) tend to validate well, in those studies that compare experimental results with trait ratings for the same set of subjects (Carter et al., 2012) or compare behavior ratings with trait ratings (Vazire et al., 2007), (b) are predictive of real-world outcomes of interest such as rank acquisition, breeding success, trainability, or immune function (Gosling & Vazire, 2002; Gosling & Mehta, 2013), (c) have factor structure similar to that of factors produced by coding of behavior (Gosling & Mehta, 2013), and (d) are generally more reliable for assessing personality across a broad range of contexts than are direct scorings of behavior (Vazire et al., 2007). Thus, worries that human observer trait ratings of animals' personality traits are merely a reflection of anthropomorphic preconceptions have largely been laid to rest by leading researchers in the field of animal personality who have compared multiple methods for personality assessment (Gosling & Vazire, 2002; Kwan et al., 2008; Gosling & Mehta, 2013), at least for studies in which ratings are conducted by people who know the animals very well, and in which multiple raters assess each individual.

Personality ratings had been developed for the Lomas Barbudal population in a prior study of personality stability in white-faced capuchins (Manson & Perry, 2013), which describes the data collection and analysis procedure in far more detail. In this prior study, observers who contributed data to the long-term database (field assistants, PI's, and graduate students) and who knew the monkeys well (typically for at least a year of full-time data collection) completed a 26-item questionnaire (see Table 1 of Manson and Perry (2013)), rating the personality traits for every monkey from the groups they knew well. Raters were instructed never to discuss their ratings with other researchers. Twenty-four of these items had high enough interobserver reliability to use in analysis (i.e. an ICC [3,k] $\geq$0.70, with a mean ICC [3,k] of 0.82).

Each monkey was rated by at least 3 raters, and sometimes by as many as 42 raters, and the mean values for each monkey for each item were computed. Manson and Perry (2013) used principal component analysis to extract five personality factors, of which two, Extraversion and Neuroticism, are used as independent variables in the current analyses. As is usual in animal personality research, these two terms are not used in precisely the same way that they are (imprecisely) used in standard English; nor do they mean precisely the same thing as they do in any study of human personality. Rather, they are defined as the linear combination of the scores on individual questionnaire traits/items weighted by the loadings of those items on those components in the principal component analysis, as described below; these components are labeled Extraversion and Neuroticism because of the close resemblance that these factor structures have to similarly named factors in

human personality research. Individual items loading heavily on Extraversion in our study included *socially intelligent*, *aggressive*, *sociable*, *persistent*, *meddlesome*, *assertive*, *popular*, *domineering*, *not fearful*, and *attentive to others.* Items loading heavily on Neuroticism included *reactive*, *intolerant/irritable*, *alert*, *aggressive*, *impulsive*, and *not relaxed* (i.e. *tense/anxious*). Further details about inter-observer reliability, the procedure for retaining components, correlations between components, and temporal stability in scores are available in Manson and Perry (2013). Consistency across three age categories (6-8 years, 8-10 years and 10-12 years) was examined. Extraversion was highly stable between ages 6-12 (i.e. late adolescence and early adulthood), whereas Neuroticism was the least stable dimension and failed to show significant stability between the 6-8 year category and the and 10-12 age category (though it was stable from 6-8 to 8-10, and from 8-10 to 10-12).

For the current study, it was important that we use only ratings from before the events we were trying to predict, so as to avoid circularity. Thus, we used only ratings from the period of life before natal emigration (for the analyses predicting emigration age) or before a male became alpha male for the first time (for the analysis predicting the timing of acquisition of alpha status for the first time). From these ratings, we calculated the unit-weighted factor scores for Extraversion and Neuroticism of 54 males (Manson & Perry, 2013). Graphs showing scatterplots of the personality variables plotted against the three outcome variables, using sample sizes from the single predictor analyses, are available in the supplementary information (Figures 1-4).

Statistics:

Cox proportional hazard models were used to determine what factors predicted (a) the time to males' first emigration from their natal groups, and (b) the time between birth and males' first acquisition of alpha male status. Both models used the following predictor variables: (a) extraversion, (b) neuroticism, (c) the proportion of the male's first 5 years of life in which his father co-resided with him (termed 'paternal co-residence length'), and (d) the percentage of time that males spent playing during months 7-60 of their juvenile phases. The number of alpha male turnovers during the male's first 5 years of development was used as an additional predictor variable for the models predicting age of natal emigration, and the age of natal emigration was used as an additional predictor for age of acquiring alpha status.

The predictor variables were tested both individually and in combination with one another (i.e. multivariate models). Multivariate models permit estimation of predictor effects that have been adjusted for the effects of the other predictors in the model. These adjusted effects can be quite different from the corresponding unadjusted effects from simple (single-predictor) regression models, particularly when the predictors are correlated (i.e. exhibit multicollinearity), as some of them are in this data set. Because we did not have all predictor variables for all subjects, sample sizes were much smaller for the models with multiple predictor variables than for the single predictor variable models (see Table 1), particularly for play

experience, emigration age, father presence and number of alpha turnovers. Data points were discarded if ages were too inaccurate to meet the following criteria: age of emigration had to be known to a precision of 0.5 years, and age of becoming alpha male had to be known to a precision of 0.55 years. Sample sizes and distribution of variables used in each model are presented in Table 1 (and broken down by whether the outcome variable of interest has occurred or not, in Supplementary Table 1). The correlations between the predictor variables in the multi-variable models are in Supplementary Information Table 2. We compared models using AIC (Akaike Information Criterion) values and BIC (Bayesian Information Criterion) values, using only the sample size of individuals for which the outcome variable and all predictor variables were measured. We present here only the multivariate model that had the lowest AIC and BIC scores for each outcome variable. We checked for multicollinearity by estimating variance inflation factors for each set of model variables, but did not detect worrisome multicollinearity as no VIF exceeded 2.0.

For those males who did not become alpha males during the study, the last date on which they were observed in the census data was used as the end date, i.e. the last date in these right-censored data points by which males definitely still had not become an alpha male. Only males whose life history had been documented since birth (so that we were certain that the first alpha male tenure observed was their first alpha tenure) were included in the analysis.

Statistical analyses were executed in Stata 14.0.

(Table 1 here)

Results:

Qualitative description of males' early "careers":

Young males experience a complex social environment during their infancy and juvenile periods, characterized by frequent rough-and-tumble play, primarily with other young males and subordinate adult males. The period between birth and the first alpha male takeover (or natal emigration) is a life phase during which males have a "safe haven" for growing, acquiring fighting and social negotiation skills (during play), and developing relationships with other natal males who may co-migrate with them. There is considerable variation between groups in the amount of play time, the amount of aggression received, the average relatedness of potential co-migrants, and the variety of social partners available to interact with. Most of this variation stems from the recent history of stability in the alpha male position: when a single alpha maintains his position for several years on end, there are lower rates of severe aggression, infant survival is high, there are large numbers of paternal half sibs, and the consequence of having high infant survival is that there will be plenty of (closely related) play partners who then are likely to become co-migrants. Unless a male has experienced an influx of immigrant males, his first experience in forming new relationships is likely to be when he leaves the group and attempts to enter a new group. At Lomas, males are never observed attempting their natal emigration on their own; they disperse initially with playmates from their natal group, who are on average related to them at approximately the level of half-sibling (Perry 2012). Males usually (though not always) emigrate before they attain

full body size. It is the impression of researchers both at Santa Rosa (Jack et al., 2014) and at Lomas (pers. obs.) that males can keep growing until about age ten years, but that there is wide inter-individual variation in growth rates, and that a rise to alpha status is often accompanied by "bulking up," particularly in the shoulders and mandibular region, so there might be age-related variation in physical strength that increases during the range of emigration ages

Males who are co-migrating typically are highly tolerant of one another, and it is hard to discern dominance rankings among members of an all-male group until they emigrate into a group with females, at which time they begin to fight amongst themselves. Sometimes there is a prolonged "visiting" phase in which co-migrants make quick visits to other groups, interspersed with visits to their natal group or time spent as an all-male group. Encounters with new groups are very dangerous, and dispersing males often receive bad wounds during their initial visits, inflicted primarily by resident males of the groups they are visiting. Arrival in a new group creates many new social challenges for males: they need to figure out which of the local resident males they are capable of defeating, develop new alliances with resident males who might help them overthrow the current alpha male, and forge relationships with new females, whose tolerance is required for access to feeding patches and whose support and cooperation will likely be helpful for advancing their rank. Females are initially hostile to new males, presumably because they represent a threat to their infants, and female-female coalitions against incoming males are common. There is variation in the way in which males enter the group: some start by playing with juvenile males on the edge of group, or grooming with

peripheral females; others boldly challenge resident males at the outset. A cluster of co-migrating male relatives may span ten years of age and thus a wide range of competitive abilities. Usually co-migrants support one another against the residents, at least initially, but co-migrants who formerly got along well develop conflicts amongst themselves once they have to compete with one another for the breeding position, causing some to leave the group and others to side with the residents of their new group against their own male relatives. These conflicts among co-migrant brothers usually take place in the immediate aftermath of a takeover, after which time they cooperative effectively for a few years; but these conflicts can erupt again many years later, with brothers overthrowing one another. Although there can be complete replacement of male membership during a takeover, it is often the case that at least some of the residents remain in the group following the takeover by incoming migrants. Further description of the variation in males' strategies and circumstances during different phases of their life histories can be found in (Perry & Manson, 2008; Perry, 2012).

What factors affect the timing of emigration from the natal group?

In a sample of 55 males of known maternity for which we had accurate emigration dates, the mean age of natal emigration was 6.4 years, ranging from 1.2-11.3 years. In 49 of these cases, the dispersal event was witnessed, and in six, the males were presumed to have dispersed outside the study area rather than dying because they disappeared simultaneously with a related male who was also of

migration age; excluding these six males caused the mean natal emigration age to drop to 6.2 years. When tested singly (Table 2a, Fig. 1), the only predictor variable that achieved significance at the P=0.05 level was percent time that the father co-resided with the male in his first five years of life. The effect of increasing paternal co-residence by 1% causes a ~1% decrease in the rate of emigration, i.e. increases the time to natal emigration.

Multivariate models were created using all possible combinations of variables, using a data set of 38 cases for which we had information on all 5 variables, and we compared the models via AIC and BIC values. The best-fit model (Table 2b) was the one that incorporated all predictor variables except for play. As predicted, males stayed significantly longer in their natal groups if their fathers were co-resident for longer, and they emigrated significantly earlier if there were larger numbers of turnovers. An increase of one alpha turnover caused a 5% increase in the rate of natal emigration. Contrary to our predictions, more extraverted males emigrated significantly later; a one unit increase in extraversion (representing 70% of the observed range of extraversion) was associated with a 79% decrease in the rate of emigration. More neurotic males remained significantly longer in their natal groups, with one unit increase in neuroticism (representing 77% of the observed range of neuroticism) being associated with a 81% decrease in the rate of emigration. These effects were consistent in their direction (though not their significance level) in all multi-variable models tested. There was no significant effect of "percent time playing" on emigration age in the full model, or in any other model tested.

Because breeding males (i.e. fathers) are typically the alpha males, and alpha males are usually (though not always) evicted during alpha male turnovers, father co-residence and the number of alpha male turnovers were negatively correlated with one another (r= -0.25). Father co-residence was negatively correlated with extraversion (r= -0.26) and neuroticism (r=-0.14). Higher numbers of alpha turnovers were positively associated with greater extraversion (r=0.22) and greater neuroticism (r=0.31).

(Table 2a,b and Figure 1 here)

What factors affect the timing of first acquisition of alpha status?

For the ten males who were included in these analyses (i.e. had sufficient accuracy in age estimates and data on the relevant predictor variables), the mean (and median) age of becoming alpha male for the first time was 10.7 ±1.8 years, ranging from 8.2 to 14.6 years. Figure 2 shows, for those males with sufficiently accurate data on the timing of emigration age and first rise to alpha status, the timing of both of these events. Extraversion (Fig. 3) was the only variable that emerged as significant in any of our models, with more extraverted males acquiring alpha status significantly earlier in life in all models; the effect of extraversion was independent of emigration age. Father presence and time spent playing were non-significant in all models and also inconsistent in the direction of their effects. Males who emigrated later in life also became alpha males later in life, though these effects

were non-significant. Males who were more neurotic were slightly more likely to become alpha males sooner, but this effect was not significant in any of the models either. Table 3a shows the results of the models that had a single predictor variable. The model in which father presence was the predictor variable violated the assumptions of the proportional hazards test and is not presented here, but it was clearly not significant (P=0.74). Table 3b shows the best fit multivariate model, which includes extraversion, neuroticism and emigration age.

(Table 3a,b and Figures 2-3 here)

Discussion:

It has been well established that the most effective route to achieving reproductive success for a male capuchin monkey is to become the alpha male of a group in which there are large numbers of females who are not closely related to him (Perry, 2012). Thus, the best strategy for achieving high lifetime RS is likely to be to acquire the alpha position as early as possible and to retain it for as long as possible, preferably in a group composed of unrelated females. This paper examines the factors that are associated with earlier natal emigration and rapid acquisition of alpha status.

What factors affect the timing of emigration from the natal group?

We had expected that more extraverted males would be less fearful of striking out on their own and exploring new groups, and hence would emigrate sooner than more introverted monkeys. Contrary to our predictions, more extraverted males stayed in their natal groups longer. It is not clear to us by what mechanism this occurs. Perhaps males who are more extraverted feel more comfortable with the social environment in their natal group (e.g. because they have more playmates and better relationships with potential mates), and therefore feel less compelled to leave. In the future, when we have a larger behavioral data set to work with, we will test whether more extraverted males are also better at attaining higher rank, developing alliances, and attaining more breeding opportunities in the natal group. More neurotic males were also more likely to emigrate later. One possible explanation is that more neurotic males defer emigration because they are more anxious about leaving home and about developing relationships with new monkeys; this would be a rational fear, given the high frequency with which dispersing males are wounded.

Males were more likely to stay longer in the natal group if their father stayed longer, and they were more likely to leave early if their early life was characterized by more frequent alpha male turnovers. Because alpha males father most of the offspring, an alpha male turnover generally means eviction of the father of most of the young males. These results are consistent with what we know from the Santa Rosa population of white-faced capuchins. There, the best predictor of age at dispersal is the length of time that a male has co-resided with the male who was alpha at the time of his conception (i.e. the probable father, though genetic paternity

was not known in that data set); this variable explained 15% of the variance in their model, but was nonsignificant when one outlier was removed (Jack et al., 2011). At Santa Rosa, natal dispersal was 18.7 times more likely to occur in the aftermath of an alpha male turnover than at other times (Jack et al., 2011). At Lomas, the bonds between fathers and their sons are often strong, particularly once the sons are old enough to participate in intergroup encounters. We have even seen sons co-emigrate with their father after the father is deposed from the alpha position. It is not clear whether the association between paternal co-residence and timing of natal dispersal is due to the strength of the father-son bonds, or to persecution of natal males by immigrant males who attain alpha rank. It has been suggested (Fedigan & Jack, 2004) that the risk of being killed by the new alpha and his allies is too great to permit resident males to remain as subordinates at Santa Rosa. At Lomas, for reasons that are not yet clear, we see more cases of incomplete male replacement following takeover events (i.e. more cases in which some subset of the natal and other resident males remain in the group after an alpha replacement from the outside) than are seen in the Santa Rosa population. Further analysis would be required to determine the mechanisms by which males decide whether to stay or leave in the aftermath of a takeover.

What factors hasten the initial rise to alpha status?

The most consistent effect to emerge from this set of analyses was that more extraverted males attained alpha status sooner; this was a significant effect in all

models. It is easy to see how extraversion might enhance ability to become alpha, as a more self-confident and social male might be less inhibited about challenging a higher-ranking animal, and indeed all of the traits that loaded positively on Extraversion (see Material and methods) are traits typically associated with leadership roles. Our analysis of personality (Manson & Perry, 2013) revealed that the capuchin variety of extraversion is not the same thing as playfulness, and extraversion also had an impact on age of becoming alpha even when controlling for the variable "percent time spent playing." Neuroticism had a nonsignificant tendency to hasten rise to alpha status in all of the multivariate models in which it was included and always had a much smaller effect size than extraversion. It is not clear how neuroticism might help, as many of the contributing traits (e.g. reactivity, intolerance/irritability, impulsivity) seem inconsistent with a successful political strategy. Aggressiveness (a trait that loads heavily on both extraversion and neuroticism) seems consistent with early rise to alpha status, and it is possible that the remaining traits associated with capuchin neuroticism – alertness and tension/anxiety – might contribute to productive vigilance about monitoring the social environment, which might help males gather information regarding the best timing for staging a takeover event.

There are very few studies demonstrating a link between play in juveniles and dominance rank later in life. However, a study of yellow-bellied marmots has demonstrated a link between play outcomes in pups and dominance rank as yearlings, which attenuates over time (so that the association almost vanishes by the time they are adults) (Blumstein et al., 2013). The precise mechanism by which

play predicts later rank is as yet unknown. Brown bear cubs who play more have a greater chance of survival to independence (Fagan & Fagan, 2009), though the mechanism by which this occurs is unclear as well. Play probably develops fighting skills by improving motor control and neural connections (Bekoff, 1988; Byers & Walker, 1995; Bell et al., 2010; Pellis et al., 2010) (but see (Sharpe, 2005b) for an example of how meerkat play does NOT improve fighting skills). Play has also been hypothesized to improve social competence (Pellis et al., 2010), emotional flexibility (Fagen & Fagen, 2009), ability to manipulate others (Brueggeman, 1978), assessment of conspecifics (Pellis & Pellis, 1996), and skills in coping with novel, unexpected situations (Spinka et al., 2001). Many have hypothesized that play solidifies social bonds (Baldwin & Baldwin, 1974; Poirier & Smith, 1974; Palagi, 2006). It should be noted, however, that no association between play frequency, social cohesion and co-dispersal was observed in meerkats, the only species in which these ideas have been rigorously tested (Sharpe, 2005a; Sharpe, 2005c).

For capuchin males who need to make decisions about whom to co-disperse with (i.e. who would be best at helping them achieve a takeover in the new group), play seemed plausible as a way to practice negotiation and assessment of valuable relationships. Contrary to our predictions, time spent playing during the first five years of life in the Lomas Barbudal capuchins did not impact the absolute age at which males became alpha males for the first time. Nor did it impact age of natal emigration (where there is not even a consistent direction of influence). It is possible that more refined measurements of play experience might reveal a different outcome: for example, taking into account the diversity of play partners, or

the cumulative play experience (rather than percentage of time playing in just the first five years) might better assess the level of social experience.

Emigration age did not significantly impact the absolute age at which males became alpha for the first time. Visual inspection of this small data set hints at a non-linear relationship between these variables, with really early emigrants and really late emigrants taking longer to become alpha males than the males who emigrate closer to the median emigration age, but we do not yet have a large enough sample size of accurate data points to accurately model age as a non-linear relationship.

This data set, though quite large by field primatology standards, is still small enough that we can expect some fluctuations in the relationship between variables in the future as we continue to increase the sample size, particularly given the currently high ratio of variables to data points. Sometimes predictor variables are not significant when tested singly, but become significant in the context of a multivariable model. The multivariable models are necessary to control for the effects of other variables; however, the sample sizes are much reduced in the multivariable models, due to the necessity of measuring all variables for each male, so it may not always be the case that the multivariable models produce a clearer understanding of the impact of each variable. This is particularly true for the variable "play," which drops from a sample of N=109 in the single variable model to N=33 in some multivariable models.

Future directions:

Several interesting questions about males' early careers remain to be resolved, due to lack of sufficient data and due to the analytical challenges of trying to understand the interplay between many variables in a dynamic system. Although this is a large data set by primatological standards, it is nonetheless the case that a large proportion of the life histories documented here remain incomplete even after 25 years of observation, leaving us with small sample sizes of individuals for which all variables can be measured. Ideally, we would want to know the impact of the variables measured in this paper on lifetime reproductive success, but the number of males for whom we have such information is still too small to warrant quantitative analysis. We would also like to know not only the onset of alpha status, but the proportion of the entire lifespan spent as alpha male, and the influence of personality and early play experience on the ability to prolong time spent as alpha male. The lack of influence of play on the timing of emigration and rise to alpha status was puzzling, but it may turn out that play impacts males' success in different ways. For example, when we have larger data sets on rare events such as coalitionary lethal aggression and severe wounds, we will be able to test whether play experience in the natal group better prepares males to migrate into a new group without incurring major injuries that lead to physical handicaps or death.

Additional data will help clarify the costs and benefits of different personality types. It has been suggested that selection maintains a variety of personality types because they have different fitness consequences in different environments (Penke et al., 2007). Alternatively, perhaps personality traits that exert a positive effect on

fitness during one phase of life exert a negative effect at other points in the individual's life history; e.g. life history tradeoffs between early and late reproduction result in polymorphisms with regard to strategies of risk aversion (Wolf et al., 2007). Extraversion appears to give white-faced capuchin males an advantage in attaining alpha status early in life; but if we continue to study these monkeys for longer, will we discover negative effects of extraversion, such as increased risk of early mortality due to boldness in combatting conspecific rivals or predators? Neuroticism seems to be particularly promising as a trait that is likely to be beneficial in some situations and costly in others. Further investigation of the relationship between personality traits and fitness-relevant decisions that animals make is likely to clarify aspects of the debate about why a diversity of animal personalities has evolved.

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Figures:

Fig. 1: Kaplan-Meier survival estimates for the effects of father presence on emigration age. The solid line shows the population for which the father was present >50% of the first 5 years of the male's life and the dotted line shows the population for which the father was present <50% of the male's first 5 years of life. The X-axis represents the time since the males' birth in years, and the Y-axis represents cumulative probability of survival.

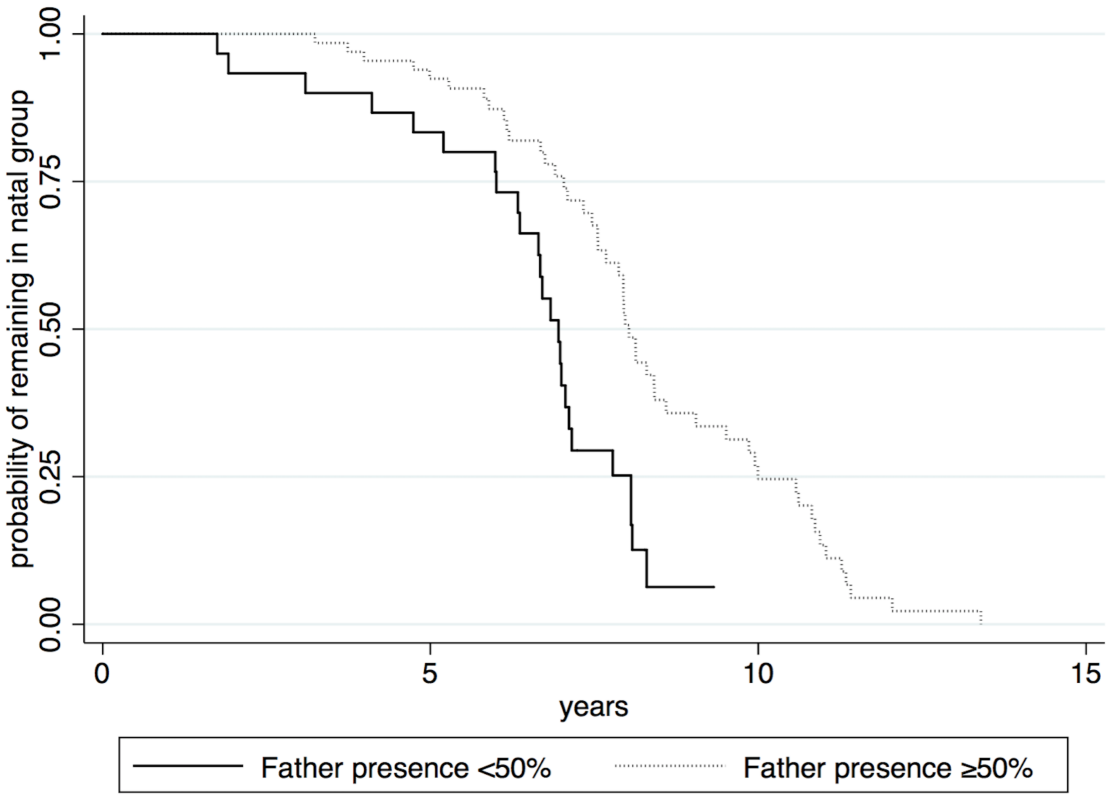


Fig.2: Timing of natal emigration and of first rise to alpha status (or age last seen without ever having become alpha) for males for whom there are accurate ages for these events. Light grey bars indicate the period between birth and natal emigration. Dark grey bars indicate the period between natal emigration and first becoming alpha male. Medium grey bars indicate the time between natal emigration and the date last seen, for males never observed to become alpha males.

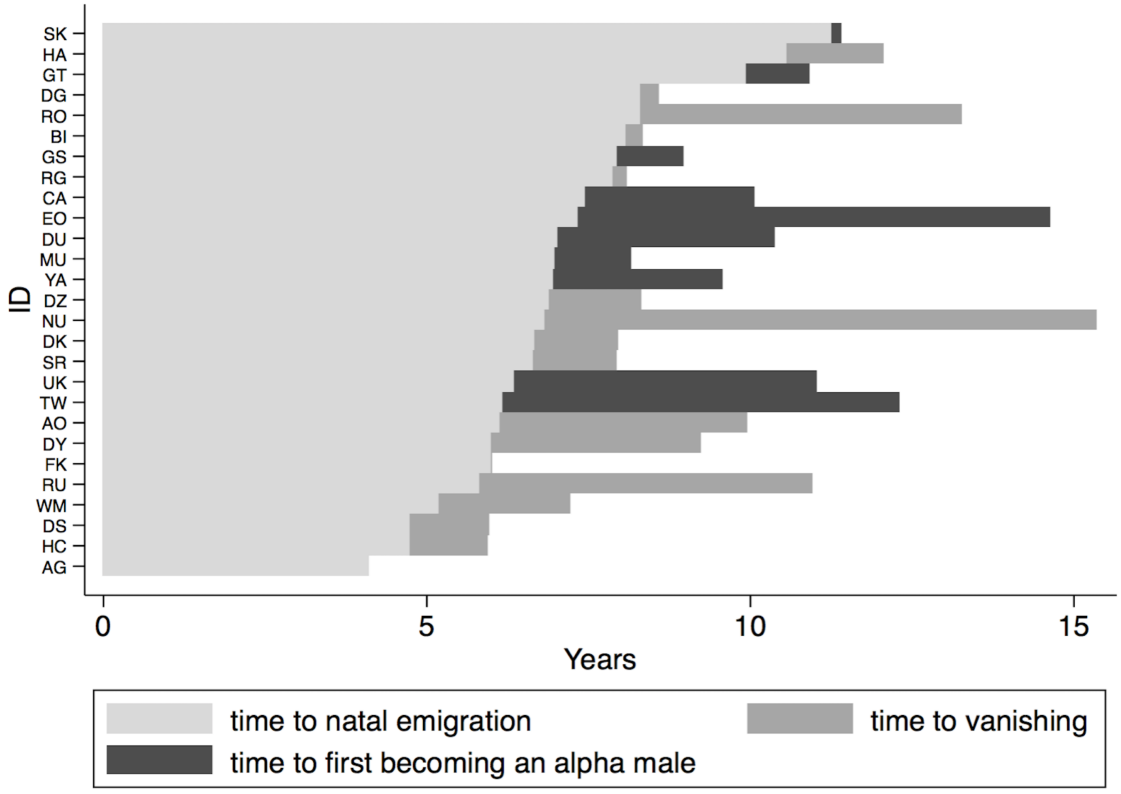


Fig. 3: Kaplan-Meier survival estimates for the effects of extraversion on the age at which males acquire alpha status for the first time. The X-axis represents the time in years, and the Y-axis represents cumulative probability of survival.

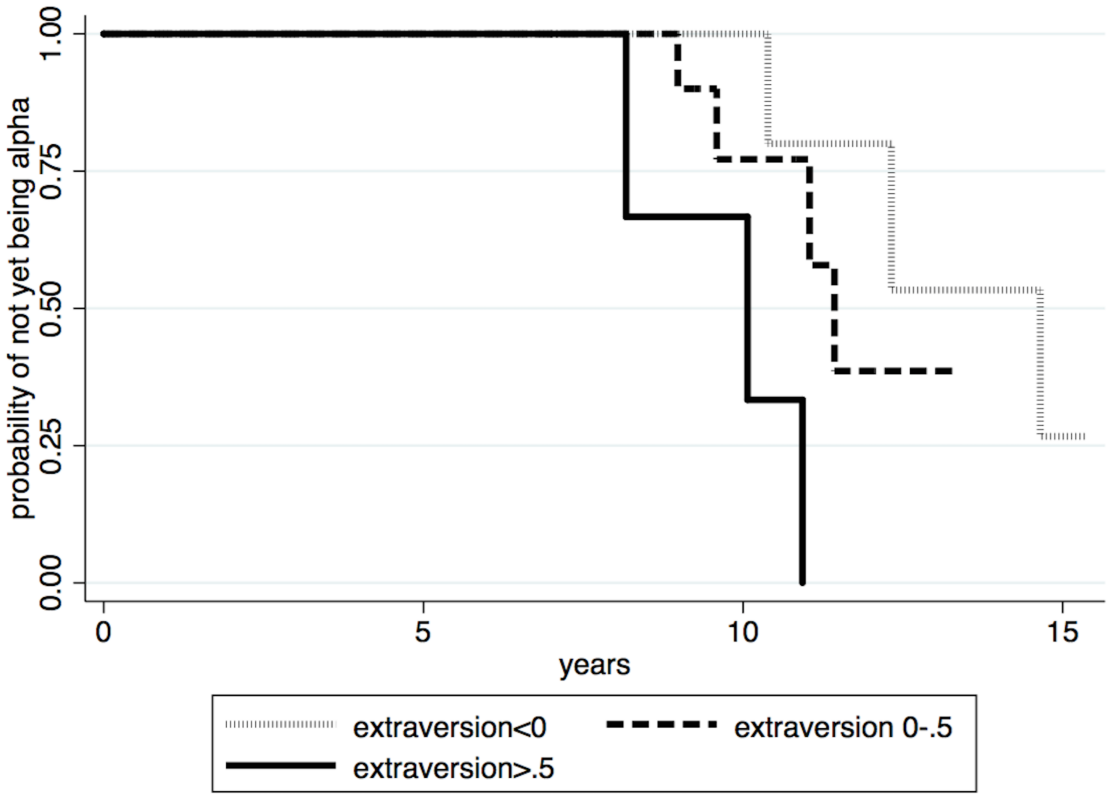


Table 1: Sample sizes and distributions of variables used in each analysis.

	Mean	SD	Min	Max	N
Age of Natal Emigration Single Variable Analyses					
Number of turnovers	3.87	6.74	0	31	149
Extraversion	0.14	0.36	-0.61	0.84	40
Neuroticism	-0.11	0.32	-0.70	0.81	40
Percent Play	6.60	3.34	1.35	28.57	109
Father presence (%)	66.51	36.86	0	100	70
Age of Natal Emigration, Multiple Variable Analyses					
Number of turnovers	6.50	9.75	0	31	38
Extraversion	0.14	0.37	-0.61	0.84	38
Neuroticism	-0.09	0.31	-0.49	0.81	38
Percent Play	7.10	2.45	1.35	14.34	38
Father presence (%)	63.44	37.67	0	100	38
Age of Becoming Alpha, Single Variable Analyses					
Age of emigration	6.37	2.3	1.19	11.27	53
Extraversion	0.13	0.34	-0.61	0.84	40
Neuroticism	-0.04	0.37	-0.82	0.81	40
Percent Play	6.44	3.38	1.35	28.57	109
Father presence (%)	64.7	37.39	0	100	71
Age of Becoming Alpha, Multiple Variable Analyses					
Age of emigration	7.20	1.83	3.99	11.27	33
Extraversion	0.14	0.37	-0.61	0.84	33
Neuroticism	-0.05	0.32	-0.76	0.81	33
Percent Play	7.23	2.23	3.24	14.34	33
Father presence (%)	62.40	38.01	0	100	33

Table 2a: Single predictor variable models in which the outcome variable is age of emigration.

Predictor variable	Hazard ratio	SE	P	CI	N
# alpha turnovers	1.03	0.02	0.066	1.00 to 1.06	149
Father presence	0.991	0.004	**0.015**	0.984 to 0.998	70
Extraversion	0.47	0.23	0.13	0.18 to 1.25	40
Neuroticism	0.42	0.21	0.089	0.15 to 1.14	40
Play	0.93	0.05	0.12	0.84 to 1.04	109

Table 2b: Best fit multivariate model in which the outcome variable is age of emigration. AIC=185, BIC=192. N=38 males, 35 of whom emigrated.

Predictor variable	Hazard ratio	SE	P	CI
# alpha turnovers	1.05	0.02	**0.029**	1.00 to 1.09
Father presence	0.989	0.005	**0.024**	0.979 to 0.999
Extraversion	0.28	0.15	**0.017**	0.099 to 0.793
Neuroticism	0.20	0.14	**0.018**	0.054 to 0.758

Table 3a: Results of single-predictor variable models in which the outcome variable is the age at which males first acquire alpha male status.

Predictor variable	Hazard ratio	Std. Error	P	95% CI	N
Extraversion	11.46	13.64	**0.04**	1.11 to 118.05	40
Neuroticism	2.32	1.71	0.25	0.55 to 9.80	40
Emigration age	0.94	0.19	0.77	0.64 to 1.40	53
Percent play	1.07	0.12	0.55	0.86 to 1.34	109

Table 3b: Multivariate model predicting age at which males first acquire alpha male status. AIC=39, BIC=43. N=33 males, 10 of whom attained alpha status.

Predictor variable	Hazard ratio	Std. Error	P	95% CI
Extraversion	40.24	56.38	**0.008**	2.58 to 626.97
Neuroticism	8.19	9.77	0.078	0.79 to 84.82
Emigration age	0.64	0.16	0.077	0.39 to 1.05

Supplementary Information

All of the figures below use the samples from the single predictor variable analyses.

Figure 1: Extraversion scores (using only pre-emigration ratings) plotted against age of first natal emigration (for emigrants, black dots) or age at which the male was last observed in the census in his natal group (for non-emigrants, open circles), N=40.

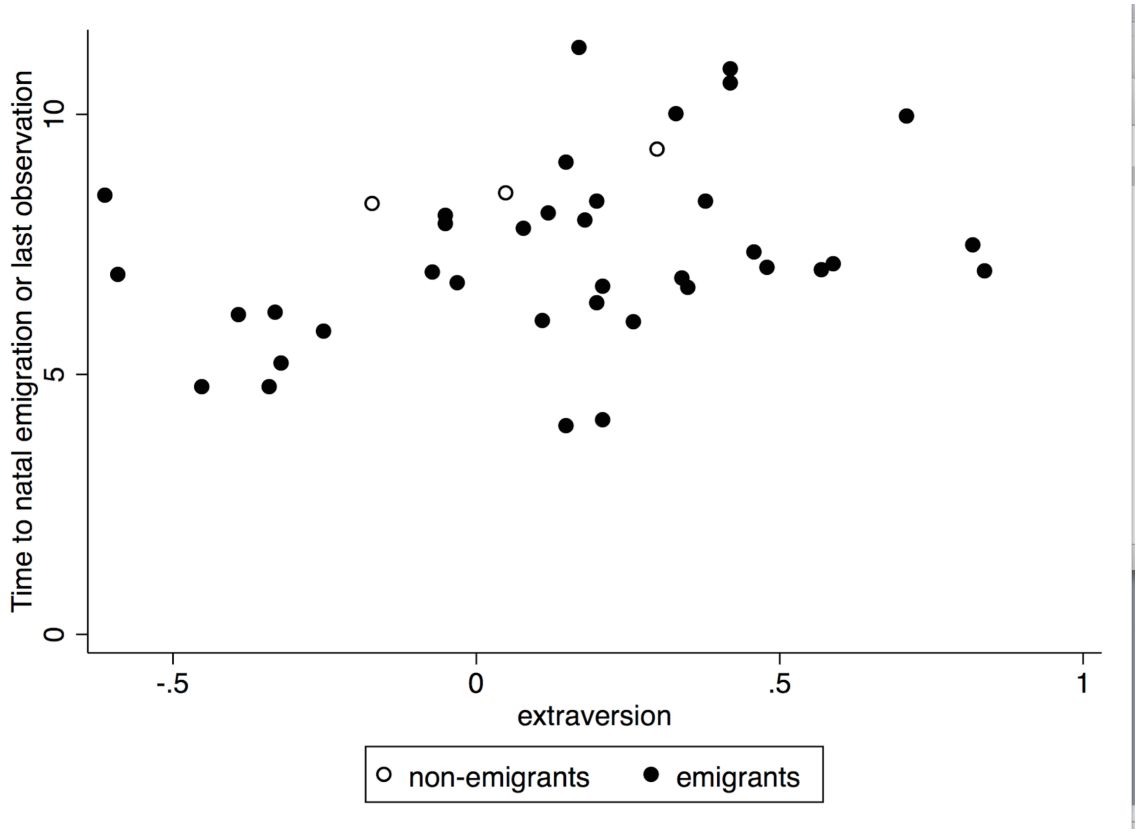


Figure 2: Neuroticism scores (using only pre-emigration ratings) plotted against age of first natal emigration (for emigrants, black dots) or age at which the male was last observed in the census in his natal group (for non-emigrants, open circles), N=40.

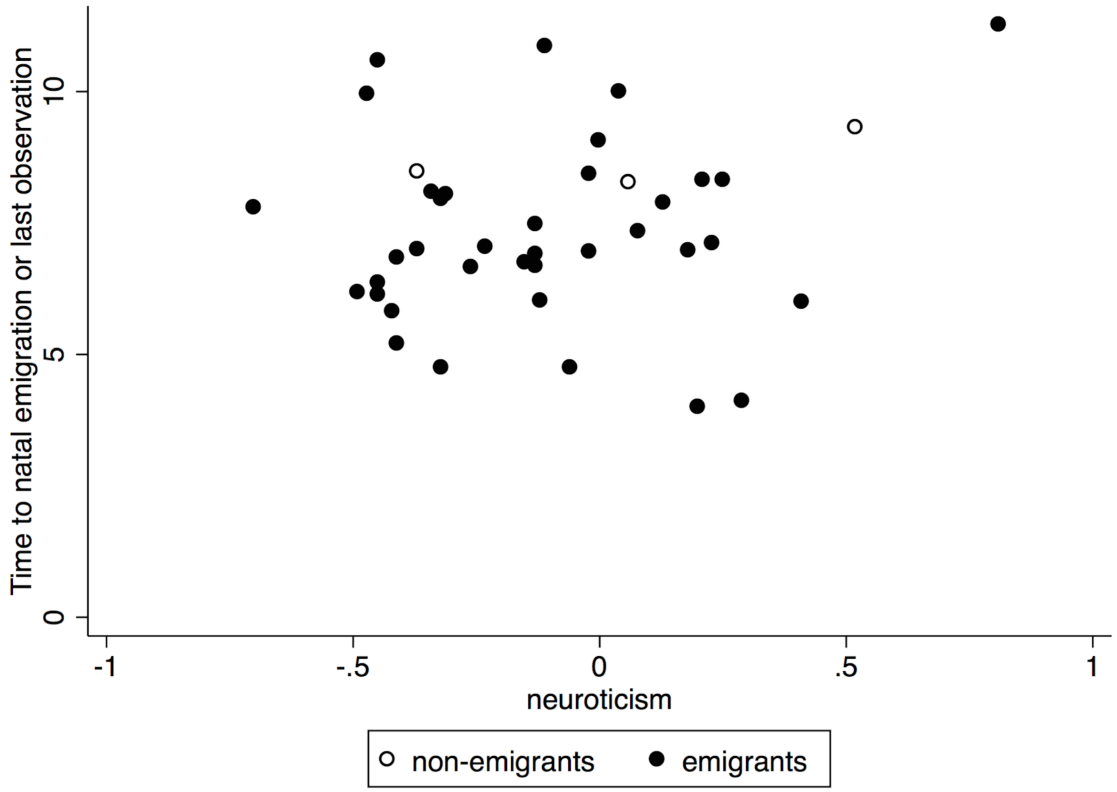


Figure 3: Extraversion scores (using only ratings prior to becoming alpha male) plotted against age of first becoming an alpha male (for alphas, black dots) or age at which the male was last observed in the census as a male who had never been alpha (for non-alphas, open circles), N=40.

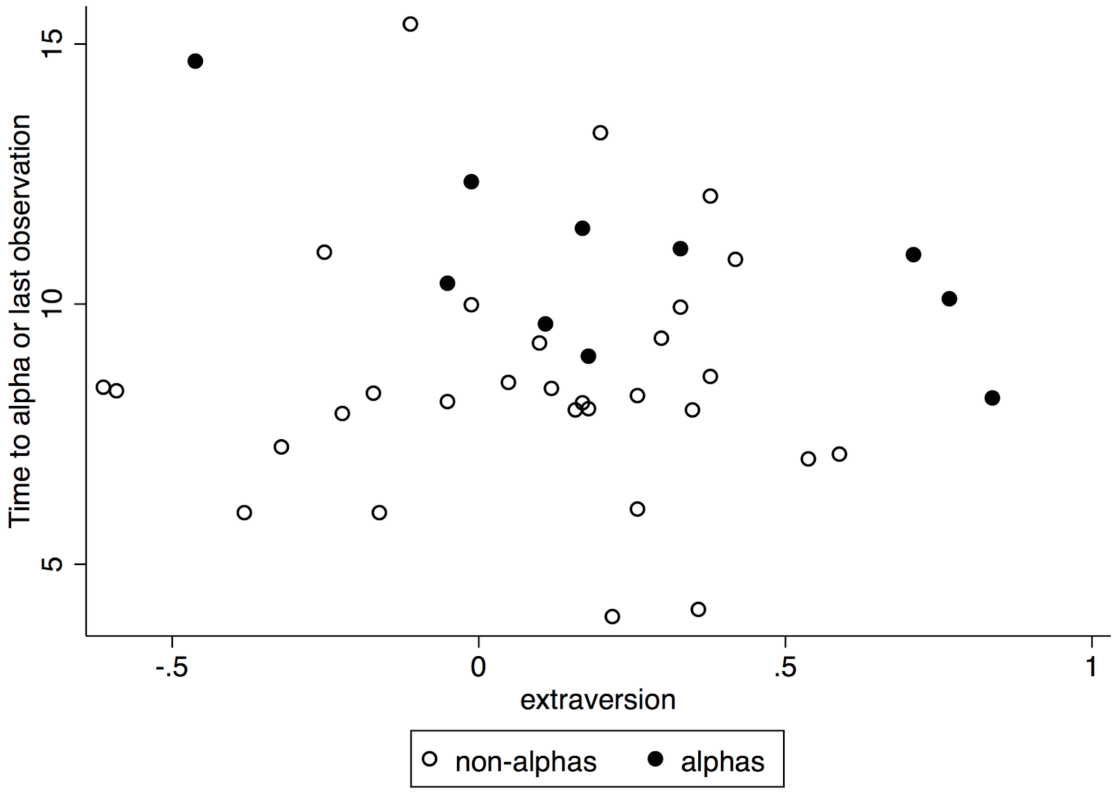
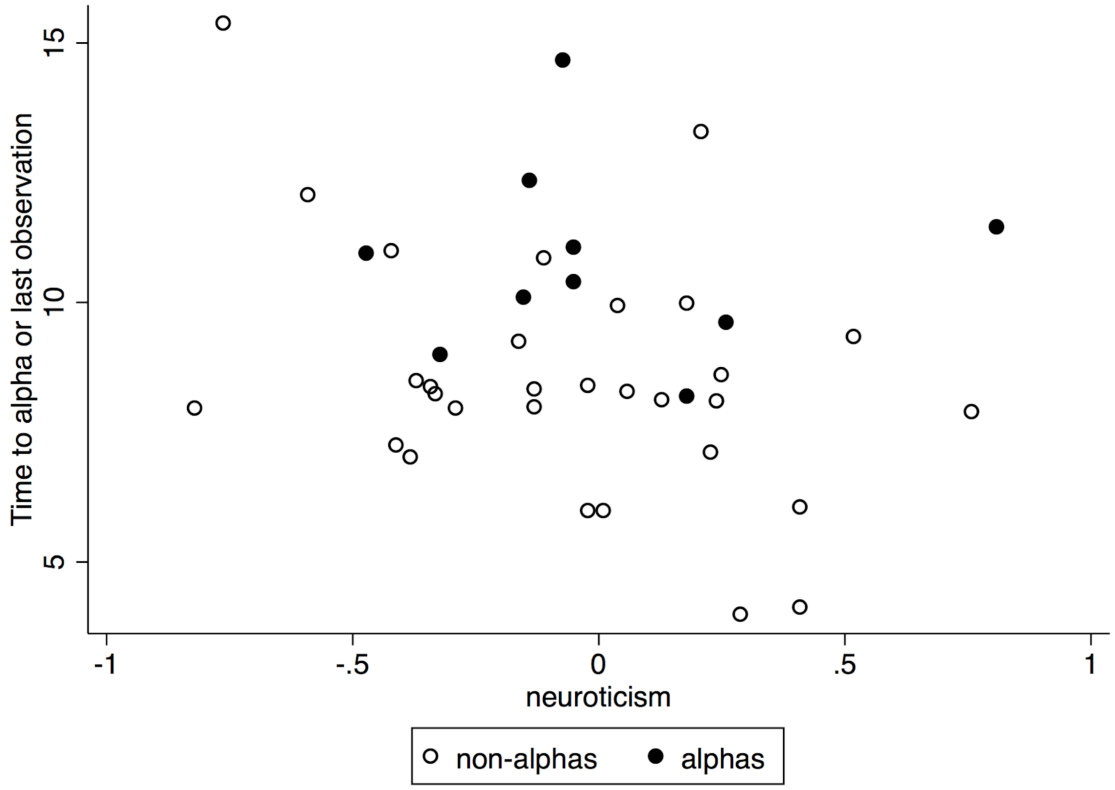


Figure 4: Neuroticism scores (using only ratings prior to becoming alpha male) plotted against age of first becoming an alpha male (for alphas, black dots) or age at which the male was last observed in the census as a male who had never been alpha (for non-alphas, open circles), N=40.



SI Table 1: Sample characteristics for variables used in multivariable analyses

	Mean	SD	Min	Max	N
Age of natal emigration analysis, all subjects					
Number of turnovers	6.5	9.75	0	31	38
Extraversion	0.14	0.37	-0.61	0.84	38
Neuroticism	-0.09	0.31	-0.49	0.81	38
Percent play	7.1	2.45	1.35	14.34	38
Father presence	63.44	37.67	0	100	38
Age of natal emigration analysis, values for emigrants					
Number of turnovers	6.6	10.16	0	31	35
Extraversion	0.15	0.38	-0.61	0.84	35
Neuroticism	-0.1	0.3	-0.49	0.81	35
Percent play	7.43	2.21	3.24	14.34	35
Father presence	64.38	37.78	0	100	35
Emigration age	7.28	1.81	3.99	11.27	35
Age of natal emigration analysis, values for males who have not yet emigrated					
Number of turnovers	5.33	1.15	4	6	3
Extraversion	0.06	0.24	-0.17	0.3	3
Neuroticism	0.07	0.45	-0.37	0.52	3
Percent play	3.17	1.73	1.35	4.79	3
Father presence	52.5	42.43	18.34	100	3
Age of becoming alpha analysis, all subjects					
Age of emigration	7.2	1.83	3.99	11.27	33
Extraversion	0.14	0.37	-0.61	0.84	33
Neuroticism	-0.05	0.32	-0.76	0.81	33
Percent play	7.23	2.23	3.24	14.34	33
Father presence	62.4	38.01	0	100	33
Age of becoming alpha analysis, values for alphas					
Age of emigration	7.75	1.62	6.17	11.27	10
Extraversion	0.26	0.41	-0.46	0.84	10
Neuroticism	0	0.35	-0.47	0.81	10
Percent play	7.96	2.56	4.71	14.34	10
Father presence	73.86	35.87	4.3	100	10
Age of becoming alpha	10.75	1.82	8.17	14.65	10
Age of becoming alpha analysis, values for males who have not yet become alpha					
Age of emigration	6.97	1.9	3.99	10.87	23
Extraversion	0.08	0.34	-0.61	0.59	23
Neuroticism	-0.07	0.32	-0.76	0.41	23
Percent play	6.91	2.05	3.24	11.33	23
Father presence	57.42	38.6	0	100	23

1

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SI Table 2: Correlations between variables in the restricted sample used for the multivariate analysis models. See Table 1 for sample sizes for each of these models.

Predictor variables	Emigration age	Age of becoming alpha
Extraversion & neuroticism	0.19	0.11
Extraversion & emigration age	--	0.28
Extraversion & play	0.13	0.31
Emigration age & father presence	--	0.32
Emigration age & play	--	0.41
Play & father presence	0.28	0.19
Extraversion & alpha turnovers	0.22	--
Neuroticism & alpha turnovers	0.31	--
Neuroticism & emigration age	--	-0.05
Neuroticism & father presence	-0.14	0.02
Neuroticism & play	-0.07	0.09
Play & alpha turnovers	-0.18	--
Father presence & alpha turnovers	-0.25	--
Extraversion & father presence	-0.26	-0.31