

1**Impact of personality traits and early life experience on timing of emigration**

2**and rise to alpha male status for wild male white-faced capuchin monkeys**

3**(*Cebus capucinus*) at Lomas Barbudal Biological Reserve, Costa Rica**

4

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

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21**Summary:**

22It is rare in studies of long-lived animals to know enough about the personalities and
23early experiences of individuals to use this information to predict their behavior
24during major life transitions in adolescence and adulthood. Here, we examine how
25personality traits and early experiences predict age of natal emigration and timing of
26first ascent to alpha status in 169 wild male white-faced capuchins studied at Lomas
27Barbudal, Costa Rica, 75 of whom emigrated and 23 of whom acquired alpha status.
28Males were more likely to delay natal emigration if they were more extraverted,
29more neurotic, if their fathers co-resided longer with them, and if there were fewer
30alpha male turnovers. More extraverted males attained alpha status sooner.

31

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

33

34**Introduction:**

35

36A thorough explication of the factors that impact male lifetime reproductive success
37necessitates investigation of males' early development and intrinsic characteristics,
38and the timing of important life history events that affect the onset of reproduction
39(van Noordwijk & van Schaik, 2001; Alberts, 2012). Although it is generally
40recognized that many important events in the life histories of individual animals are
41likely to be influenced by both personality -- i.e. those characteristics that describe
42and account for stable individual differences in behavior -- and experiences during
43early development (Dingemanse et al., 2002), it is rarely possible to document these

44relationships in the wild, particularly for long-lived animals like primates. This is
45particularly true for species in which males disperse (i.e. most mammalian species
46(Dobson, 1982; Cockburn, 1992; Wolff, 1993; Alberts, 2012)), because it is hard to
47track males once they have left their natal groups.

48 Although the relationship between male dominance rank and reproductive
49success (RS) is variable both within and between species, dominance rank is usually
50an important determinant of breeding success in mammals, including primates
51(Cowlshaw & Dunbar, 1991; de Ruiter & van Hooff, 1993; Ellis, 1995; Alberts, 2012),
52and this is particularly true in white-faced capuchins, *Cebus capucinus* (Muniz et al.,
532010). Because rank is so important for attaining RS, understanding the
54determinants of lifetime RS requires an understanding of how males rise to alpha
55status.

56 In this study of wild white-faced capuchin males, we investigate the
57relationship between two personality traits (extraversion and neuroticism) and the
58timing of two important life history events: natal emigration and first rise to alpha
59status. We also investigate the relationships between these outcomes and two forms
60of early experience: frequency of social play and social stability (as measured by co-
61residence of the young male with his father and by the number of alpha male
62turnovers during the male's juvenile phase).

63 Age at natal emigration, and age at first rise to alpha status, are expected to
64be fitness-relevant outcomes because (a) most breeding is accomplished by alpha
65males (Muniz et al., 2010), and (b) males typically first achieve alpha status after
66emigrating. In white-faced capuchins, females are philopatric and males disperse

67(Perry, 2012). Reproductive skew is high in this species, with alpha males essentially
68monopolizing breeding opportunities with females who are not their direct
69descendants (Muniz et al., 2006; Muniz et al., 2010; Godoy et al., 2016).

70 The ubiquity of coalitional aggression among capuchins (Perry, 2012) implies
71that achieving and maintaining alpha status generally requires both fighting skills
72and advanced social skills. The latter enable individuals to manage relationships
73with allies who are necessary for helping a male attain alpha status and defend his
74reproductive access to females from rival males (Perry 2012, Perry and Manson
752008). Social play has been hypothesized to hone fighting skills and also social
76negotiation skills (Bekoff, 1988; Byers & Walker, 1995; Bell et al., 2010; Pellis et al.,
772010). Thus, we predicted that males who spend more time engaged in rough-and-
78tumble play as juveniles will be capable of achieving an alpha male position more
79quickly upon entering a new group, compared to males with less play experience.

80 The form of early life experience that seems most likely to affect males'
81decision-making about how long to remain in their natal group is the stability of the
82alpha male position. Alpha male turnovers are bloody, chaotic events that typically
83result in high rates of infanticide as well as wounding or even death of other group
84members (Fedigan, 2003; Perry & Manson, 2008; Perry, 2012; Perry et al., 2012).
85Past research at Lomas revealed that 24% of takeovers were accomplished by
86groups of co-migrant males invading from the outside, and 61% were internal
87takeovers by long-term resident males (Perry et al 2011); in all of these cases, the
88takeover involved violent conflict between the old alpha male and his challenger(s).
89Sometimes the takeover is rapid, taking only a single day, and other times there is a

90phase of repeated challenges and reversals lasting for a few months. In a few cases,
91the alpha male acquired the position peacefully, when the former alpha male died of
92extrinsic causes or migrating males chanced upon a new fission product that did not
93yet have males attached to it. In all cases except for peaceful inheritance by a
94resident, infanticide was a common outcome. Previous work on the timing of natal
95dispersal in white-faced capuchins at the nearby site of Santa Rosa has found that
96natal dispersal is far more likely during the social instability period characterizing
97the aftermath of an alpha male takeover (Jack et al., 2011).

98 Intrinsic factors such as personality, health or body size may affect the types
99of strategic options available (Sapolsky, 1991), influencing decisions about the
100timing of investment in somatic vs. reproductive effort, and the tradeoffs between
101survival and reproduction. A recent meta-analysis of personality traits that
102encompassed both vertebrates and invertebrates found that bolder males, i.e. those
103willing to take more risks, had higher short term reproductive success but lower
104survival (Smith & Blumstein, 2008). Personality traits, or behavioral syndromes (Sih
105et al., 2004), may be adaptive in some circumstances but not others, and
106furthermore, individuals may lack the capacity to adjust their behavior so as to apply
107it only in the circumstances in which it is most favorable. For example, in Namibian
108rock agamas, bold males are more exploratory (which gives them access to more
109food resources) but also are excessively bold in approaching predators, which is
110probably responsible for their higher rates of tail loss (Carter et al., 2010). Very little
111research on the fitness correlates of personality traits is available from nonhuman
112primates. However, various personality traits (“niceness,” “aloofness” and “loner”) in

113baboons influence their degree of sociality and capacity to form stable long-term
114relationships (Seyfarth et al., 2012), which in turn probably influence their fitness
115(Silk et al., 2009; Silk et al., 2010).

116 Research on our study population (Manson & Perry, 2013) has revealed a
117personality structure comprising five dimensions. One of these, Extraversion (see
118methods section on personality ratings for definition of Extraversion and
119Neuroticism), encompasses three facets of human Extraversion (Costa & McCrae,
1201995): Gregariousness, Assertiveness, and Excitement Seeking. We predicted that
121more extraverted males would emigrate earlier and also become alpha males earlier,
122as these attributes would make them more confident and persistent in challenging
123dominants and in establishing new relationships outside their natal groups.

124 A second personality dimension in *C. capucinus* is Neuroticism (Manson &
125Perry, 2013), which encompasses the Anxiety, Angry Hostility, and Impulsivity facets
126(Costa & McCrae, 1995) of human Neuroticism. High levels of Neuroticism might be
127expected to impair capuchin males' ability to develop the physical competitive
128ability and social skills necessary to successfully emigrate and form the alliances
129necessary to acquire and maintain a breeding position. We base this prediction on
130findings that highly neurotic humans are more prone to psychiatric disorders and
131chronic somatic ill health (Claridge & Davis, 2001; Neeleman et al., 2002), and also
132on findings that neuroticism predicts social isolation and marital relationship
133failure in humans (Kelly & Conley, 1987). On the other hand, the increased
134impulsivity of neurotic capuchins might lead them to attempt emigration or
135challenge alpha males sooner than less neurotic males might (though these attempts

136 would be successful only if the male were physically and socially prepared to
137 compete successfully in a new situation at that age). The anxiety component of
138 neuroticism might serve a useful adaptive function for capuchins, causing them to
139 monitor their rivals or detect predators more effectively.

140 It is likely to be the case that emigrating sooner increases the chances of
141 acquiring a breeding position earlier in life (thereby possibly extending his total
142 number of reproductive years), but this is not necessarily the case, depending on
143 both intrinsic characteristics of the male (e.g. current body size, health and age) and
144 the quality of his demographic situation in the natal group in comparison to his
145 dispersal options (e.g. how many males are ahead of him in a reproductive queue, or
146 how many non-kin females are available as potential breeding partners). Males with
147 low competitive ability for their age might, for example, benefit from staying longer
148 in the natal group and/or deferring a competitive push for an alpha male position
149 until their body mass and fighting skills have improved (Heg et al., 2011) . The natal
150 group is likely to be a “safe haven” (Kokko & Ekman, 2002) where males can
151 continue to invest in somatic effort if males’ parents or other tolerant close kin
152 remain in the group longer. If the natal home range is of particularly high quality and
153 a natal male stands a good chance of inheriting breeding access to this group, he
154 may do better to delay dispersal rather than to disperse and breed earlier in a group
155 that has a lower quality home range and worse breeding opportunities (Stacey &
156 Ligon, 1991; Heg et al., 2011). Also, staying longer with kin might afford indirect
157 fitness benefits if there are opportunities to defend the natal group from infanticidal
158 males or provide alloparenting to closely related immatures.

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

162

163 *Predicting age of emigration:*

164

165 We predicted that more extraverted males would leave earlier (being less
166 intimidated by novel social situations and more skilled at forming new
167 relationships). We had no specific directional prediction for neuroticism; although
168 we expected neuroticism to cause monkeys to be less adept at relationship
169 formation, these circumstances might either cause earlier emigration (due to low
170 satisfaction with relationships in the natal group) or later emigration, due to lack of
171 skill in forming new relationships outside the natal group. The impulsivity
172 dimension of neuroticism might promote earlier emigration, whereas the anxiety
173 dimension might promote later emigration. We predicted that males would emigrate
174 sooner if there were frequent alpha male turnovers in their groups during their first
175 five years of life, since such turnovers are associated with higher incidents of
176 wounding of group members (and presumably a more stressful social environment
177 overall). We predicted that males would stay longer in natal groups if their fathers
178 stayed in the group longer. One reason to predict delayed emigration when fathers
179 remained in the group longer is that longer paternal residence probably means that
180 a potential emigrant had a larger number of younger paternal siblings in the group.
181 Not only would these younger siblings possibly become co-migrants who aid one

182another later in life, but there might also be indirect fitness benefits derived from
183contributing to group defense, and thereby promoting the survival of paternal
184siblings. Another reason to stay is that a father (even a subordinate father) might
185provide continued protection and coalitionary support to sons even if he were not
186the alpha male, thereby increasing the benefit:cost ratio of staying longer to invest in
187somatic effort.

188

189*Predicting age of first acquisition of alpha status:*

190

191Males face a major social challenge when they first emigrate and seek a position
192where they could breed. Perhaps for the first time in their lives, they must form
193alliances and competitive relationships with monkeys who are unfamiliar to them.
194Their ability to solve these challenges determines whether they succeed in acquiring
195alpha status and hence an early opportunity to breed. Greater amounts of social
196experience and fighting skills (as assayed by percentage of time spent engaging in
197rough-and-tumble play during the first five years of life) were hypothesized to
198predict earlier success at becoming an alpha male. We also hypothesized that more
199extraverted males would achieve alpha status earlier, for the following reasons
200(which we couldn't test directly in a quantitative way): We thought they would be
201better at forging alliances both with potential allies from the natal group and with
202resident males and females in the group to which they disperse, and be more
203confident about attempting takeovers. We were less certain what to predict about
204neuroticism, though we suspected it might be relevant: either more neurotic males

205 might be more (productively) vigilant, or their anxiety levels might prevent them
206 from achieving the social competence necessary to become alpha males.

207

208 **Material and methods:**

209

210 *Study site and subjects:*

211

212 The data in this study were collected as part of a 25-year study of the behavioral
213 ecology of white-faced capuchins at Lomas Barbudal, Costa Rica and surrounding
214 areas that began in 1990 (see Perry 2012 and Perry et al. 2012 for further details
215 regarding the demography and social dynamics of the Lomas Barbudal population
216 and the history of the study). This study used data collected up through November
217 2015. The social groups included 10 stable groups including both males and females
218 that were regularly monitored, and five multi-male/multi-female groups that were
219 more sporadically monitored, plus various all-male groups. This dataset includes
220 data from 169 males born into nine social groups. Natal emigration was observed for
221 75 of these males, and 23 attained alpha status during the study period. Data on
222 personality traits and on father presence or play experience during the juvenile
223 phase were available for subsets of this larger data set.

224 Past research on *Cebus capucinus*, from the two long-term sites where male
225 life histories and social relationships have been studied (Lomas Barbudal and Santa
226 Rosa), has revealed that this is a female-philopatric species in which males disperse,
227 often with other males who are frequently their kin (Jack & Fedigan, 2004a; Jack &

228Fedigan, 2004b; Perry, 2012; Wikberg et al., 2014). The mean group size at Lomas is
22918.8 (range: 5-40), with adult male:female sex ratios varying from 0.22 to 1.44
230(Perry, 2012). Most groups contain multiple adult females and multiple adult males,
231but one-male groups are sometimes observed (though they eventually attract
232additional males).

233

234*Demographic data:*

235

236Whenever monkeys were encountered, researchers noted the identities of all
237monkeys that were in visual or auditory contact of one another as being in the same
238social group. Most social groups encountered were composed of relatively stable
239sets of individuals, but lone monkeys and clusters of co-traveling males were noted
240also. Census data were collected systematically in this way, on checksheets designed
241for this purpose, beginning in July 2006 and continuing to the present. Prior to that
242time, notes about contact with monkeys were kept in field notebooks and also
243recorded in the behavioral data; these data were later extracted from these sources
244to create a census database. The number of monkeys and social groups increased
245over time, and the number of days that each group was followed per month varied as
246a function of the ratio of on-site researchers to social groups. In general, effort was
247made to census each primary research group at least once per month. When there
248was evidence of social tension among males and hence instability in male
249dominance ranks, that group was censused more frequently, thereby reducing the
250possibility of missing rank changes.

251

252 *Determination of dominance ranks:*

253

254 Past research on the rank relations and social dynamics of male capuchins (Perry,
255 1998b; Perry, 1998a) indicates that the best predictors of dominance rank are
256 spontaneous submissive behaviors (avoidance and cowering) in the context of
257 dyadic social interactions. In this species, alpha males are typically readily
258 distinguishable from subordinate males not only by the direction of these
259 submissive behaviors, but also because, compared to subordinates, they generally
260 exhibit far more piloerection, display behaviors, vocalizations and urine-washing,
261 and they occupy more spatially central positions within their group (Perry, 1998b;
262 Perry, 1998a; Campos et al., 2007). Whereas alpha males are normally easy to
263 identify, the rank relations between subordinate males are far murkier and cannot
264 always be readily detected (Perry, 1998b; Schoof & Jack, 2014). There were some
265 cases of alpha male rank reversals occurring during observation gaps, and of course
266 it is possible that there were multiple turnovers in some of these longer gaps.
267 Nonetheless, if there was an observation gap bounded by days in which the same
268 male was alpha male at both ends, we assumed continuity in the alpha male position
269 during that gap, and if there was a different male who was alpha at each end of the
270 gap, we assumed just one turnover. In cases for which the date of the turnover was
271 not known precisely, we used the average between the earliest and latest possible
272 date as the date of the turnover.

273

274 *Measurement of play:*

275

276 The percentage of time that males spent playing during the months 7-60 of their
277 lives was determined by calculating the proportion of scan samples in which the
278 monkey was engaged in rough and tumble play (i.e. play chasing, hitting, wrestling
279 and biting, either quickly or in slow motion). Scan samples were collected either as
280 group scans, for the 43 males whose juvenile periods occurred after January 2001
281 (average 1460 ± 944 scans/male, range 65-3509), or as instantaneous scans during
282 focal follows for 7 males whose juvenile periods occurred prior to 2001 (average of
283 75 ± 17 scans/male, range 53-102). During group scans, each monkey's activity was
284 recorded during the first instance in which the monkey was seen, at intervals no
285 closer than 10 minutes. During focal follows in pre-2001 data, instantaneous scans
286 were performed at 2.5-minute intervals. Because there was no clear change in time
287 spent playing between months 6-60, these data were pooled. For the analysis in
288 which play was used to predict age of emigration, the scan data collected post-
289 emigration were dropped from the analysis. No male became alpha male during his
290 first five years of life, and hence none of the scan data used to calculate play
291 experience were from males who had already become alpha.

292

293 *Personality measures:*

294

295 In the early days of animal personality research, there was a tendency to rely more
296 on behavior ratings than observer ratings of personality traits in order to

297characterize individuals' personalities, because of a suspicion that humans' ratings
298of another species' personalities might introduce anthropomorphic bias. However, a
299growing body of work in the rapidly expanding field of animal personality research
300has revealed that human observer ratings of animal personality traits are not only
301logistically more feasible in a wide range of circumstances, but also (a) tend to
302validate well, in those studies that compare experimental results with trait ratings
303for the same set of subjects (Carter et al., 2012) or compare behavior ratings with
304trait ratings (Vazire et al., 2007), (b) are predictive of real-world outcomes of
305interest such as rank acquisition, breeding success, trainability, or immune function
306(Gosling & Vazire, 2002; Gosling & Mehta, 2013), (c) have factor structure similar to
307that of factors produced by coding of behavior (Gosling & Mehta, 2013), and (d) are
308generally more reliable for assessing personality across a broad range of contexts
309than are direct scorings of behavior (Vazire et al., 2007). Thus, worries that human
310observer trait ratings of animals' personality traits are merely a reflection of
311anthropomorphic preconceptions have largely been laid to rest by leading
312researchers in the field of animal personality who have compared multiple methods
313for personality assessment (Gosling & Vazire, 2002; Kwan et al., 2008; Gosling &
314Mehta, 2013), at least for studies in which ratings are conducted by people who
315know the animals very well, and in which multiple raters assess each individual.

316 Personality ratings had been developed for the Lomas Barbudal population in
317a prior study of personality stability in white-faced capuchins (Manson & Perry,
3182013), which describes the data collection and analysis procedure in far more detail.
319In this prior study, observers who contributed data to the long-term database (field

320assistants, PI's, and graduate students) and who knew the monkeys well (typically
321for at least a year of full-time data collection) completed a 26-item questionnaire
322(see Table 1 of Manson and Perry (2013)), rating the personality traits for every
323monkey from the groups they knew well. Raters were instructed never to discuss
324their ratings with other researchers. Twenty-four of these items had high enough
325interobserver reliability to use in analysis (i.e. an ICC [3,k] ≥ 0.70 , with a mean ICC
326[3,k] of 0.82).

327 Each monkey was rated by at least 3 raters, and sometimes by as many as 42
328raters, and the mean values for each monkey for each item were computed. Manson
329and Perry (2013) used principal component analysis to extract five personality
330factors, of which two, Extraversion and Neuroticism, are used as independent
331variables in the current analyses. As is usual in animal personality research, these
332two terms are not used in precisely the same way that they are (imprecisely) used in
333standard English; nor do they mean precisely the same thing as they do in any study
334of human personality. Rather, they are defined as the linear combination of the
335scores on individual questionnaire traits/items weighted by the loadings of those
336items on those components in the principal component analysis, as described below;
337these components are labeled Extraversion and Neuroticism because of the close
338resemblance that these factor structures have to similarly named factors in human
339personality research. Individual items loading heavily on Extraversion in our study
340included *socially intelligent, aggressive, sociable, persistent, meddlesome, assertive,*
341*popular, domineering, not fearful,* and *attentive to others*. Items loading heavily on
342Neuroticism included *reactive, intolerant/irritable, alert, aggressive, impulsive,* and

343 *not relaxed* (i.e. *tense/anxious*). Further details about inter-observer reliability, the
344 procedure for retaining components, correlations between components, and
345 temporal stability in scores are available in Manson and Perry (2013). Consistency
346 across three age categories (6-8 years, 8-10 years and 10-12 years) was examined.
347 Extraversion was highly stable between ages 6-12 (i.e. late adolescence and early
348 adulthood), whereas Neuroticism was the least stable dimension and failed to show
349 significant stability between the 6-8 year category and the and 10-12 age category
350 (though it was stable from 6-8 to 8-10, and from 8-10 to 10-12).

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

361

362 *Statistics:*

363

364 Cox proportional hazard models were used to determine what factors
365 predicted (a) the time to males' first emigration from their natal groups, and (b) the

366time between birth and males' first acquisition of alpha male status. Both models
367used the following predictor variables: (a) extraversion, (b) neuroticism, (c) the
368proportion of the male's first 5 years of life in which his father co-resided with him
369(termed 'paternal co-residence length'), and (d) the percentage of time that males
370spent playing during months 7-60 of their juvenile phases. The number of alpha
371male turnovers during the male's first 5 years of development was used as an
372additional predictor variable for the models predicting age of natal emigration, and
373the age of natal emigration was used as an additional predictor for age of acquiring
374alpha status.

375 The predictor variables were tested both individually and in combination
376with one another (i.e. multivariate models). Multivariate models permit estimation
377of predictor effects that have been adjusted for the effects of the other predictors in
378the model. These adjusted effects can be quite different from the corresponding
379unadjusted effects from simple (single-predictor) regression models, particularly
380when the predictors are correlated (i.e. exhibit multicollinearity), as some of them
381are in this data set. Because we did not have all predictor variables for all subjects,
382sample sizes were much smaller for the models with multiple predictor variables
383than for the single predictor variable models (see Table 1), particularly for play
384experience, emigration age, father presence and number of alpha turnovers. Data
385points were discarded if ages were too inaccurate to meet the following criteria: age
386of emigration had to be known to a precision of 0.5 years, and age of becoming alpha
387male had to be known to a precision of 0.55 years. Sample sizes and distribution of
388variables used in each model are presented in Table 1 (and broken down by whether

389the outcome variable of interest has occurred or not, in Supplementary Table 1). The
390correlations between the predictor variables in the multi-variable models are in
391Supplementary Information Table 2. We compared models using AIC (Akaike
392Information Criterion) values and BIC (Bayesian Information Criterion) values, using
393only the sample size of individuals for which the outcome variable and all predictor
394variables were measured. We present here only the multivariate model that had the
395lowest AIC and BIC scores for each outcome variable. We checked for
396multicollinearity by estimating variance inflation factors for each set of model
397variables, but did not detect worrisome multicollinearity as no VIF exceeded 2.0.

398 For those males who did not become alpha males during the study, the last
399date on which they were observed in the census data was used as the end date, i.e.
400the last date in these right-censored data points by which males definitely still had
401not become an alpha male. Only males whose life history had been documented
402since birth (so that we were certain that the first alpha male tenure observed was
403their first alpha tenure) were included in the analysis.

404 Statistical analyses were executed in Stata 14.0.

405

406 (Table 1 here)

407

408**Results:**

409*Qualitative description of males' early "careers":*

410Young males experience a complex social environment during their infancy and
411juvenile periods, characterized by frequent rough-and-tumble play, primarily with

412 other young males and subordinate adult males. The period between birth and the
413 first alpha male takeover (or natal emigration) is a life phase during which males
414 have a “safe haven” for growing, acquiring fighting and social negotiation skills
415 (during play), and developing relationships with other natal males who may co-
416 migrate with them. There is considerable variation between groups in the amount of
417 play time, the amount of aggression received, the average relatedness of potential
418 co-migrants, and the variety of social partners available to interact with. Most of this
419 variation stems from the recent history of stability in the alpha male position: when
420 a single alpha maintains his position for several years on end, there are lower rates
421 of severe aggression, infant survival is high, there are large numbers of paternal half
422 sibs, and the consequence of having high infant survival is that there will be plenty
423 of (closely related) play partners who then are likely to become co-migrants. Unless
424 a male has experienced an influx of immigrant males, his first experience in forming
425 new relationships is likely to be when he leaves the group and attempts to enter a
426 new group. At Lomas, males are never observed attempting their natal emigration
427 on their own; they disperse initially with playmates from their natal group, who are
428 on average related to them at approximately the level of half-sibling (Perry 2012).
429 Males usually (though not always) emigrate before they attain full body size. It is the
430 impression of researchers both at Santa Rosa (Jack et al., 2014) and at Lomas (pers.
431 obs.) that males can keep growing until about age ten years, but that there is wide
432 inter-individual variation in growth rates, and that a rise to alpha status is often
433 accompanied by “bulking up,” particularly in the shoulders and mandibular region,

434so there might be age-related variation in physical strength that increases during the
435range of emigration ages

436 Males who are co-migrating typically are highly tolerant of one another, and it
437is hard to discern dominance rankings among members of an all-male group until
438they emigrate into a group with females, at which time they begin to fight amongst
439themselves. Sometimes there is a prolonged “visiting” phase in which co-migrants
440make quick visits to other groups, interspersed with visits to their natal group or
441time spent as an all-male group. Encounters with new groups are very dangerous,
442and dispersing males often receive bad wounds during their initial visits, inflicted
443primarily by resident males of the groups they are visiting. Arrival in a new group
444creates many new social challenges for males: they need to figure out which of the
445local resident males they are capable of defeating, develop new alliances with
446resident males who might help them overthrow the current alpha male, and forge
447relationships with new females, whose tolerance is required for access to feeding
448patches and whose support and cooperation will likely be helpful for advancing their
449rank. Females are initially hostile to new males, presumably because they represent
450a threat to their infants, and female-female coalitions against incoming males are
451common. There is variation in the way in which males enter the group: some start by
452playing with juvenile males on the edge of group, or grooming with peripheral
453females; others boldly challenge resident males at the outset. A cluster of co-
454migrating male relatives may span ten years of age and thus a wide range of
455competitive abilities. Usually co-migrants support one another against the residents,
456at least initially, but co-migrants who formerly got along well develop conflicts

457amongst themselves once they have to compete with one another for the breeding
458position, causing some to leave the group and others to side with the residents of
459their new group against their own male relatives. These conflicts among co-migrant
460brothers usually take place in the immediate aftermath of a takeover, after which
461time they cooperative effectively for a few years; but these conflicts can erupt again
462many years later, with brothers overthrowing one another. Although there can be
463complete replacement of male membership during a takeover, it is often the case
464that at least some of the residents remain in the group following the takeover by
465incoming migrants. Further description of the variation in males' strategies and
466circumstances during different phases of their life histories can be found in (Perry &
467Manson, 2008; Perry, 2012).

468

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

470

471 In a sample of 55 males of known maternity for which we had accurate
472emigration dates, the mean age of natal emigration was 6.4 years, ranging from 1.2-
47311.3 years. In 49 of these cases, the dispersal event was witnessed, and in six, the
474males were presumed to have dispersed outside the study area rather than dying
475because they disappeared simultaneously with a related male who was also of
476migration age; excluding these six males caused the mean natal emigration age to
477drop to 6.2 years. When tested singly (Table 2a, Fig. 1), the only predictor variable
478that achieved significance at the $P=0.05$ level was percent time that the father co-
479resided with the male in his first five years of life. The effect of increasing paternal

480co-residence by 1% causes a ~1% decrease in the rate of emigration, i.e. increases
481the time to natal emigration.

482 Multivariate models were created using all possible combinations of
483variables, using a data set of 38 cases for which we had information on all 5
484variables, and we compared the models via AIC and BIC values. The best-fit model
485(Table 2b) was the one that incorporated all predictor variables except for play. As
486predicted, males stayed significantly longer in their natal groups if their fathers were
487co-resident for longer, and they emigrated significantly earlier if there were larger
488numbers of turnovers. An increase of one alpha turnover caused a 5% increase in
489the rate of natal emigration. Contrary to our predictions, more extraverted males
490emigrated significantly later; a one unit increase in extraversion (representing 70%
491of the observed range of extraversion) was associated with a 79% decrease in the
492rate of emigration. More neurotic males remained significantly longer in their natal
493groups, with one unit increase in neuroticism (representing 77% of the observed
494range of neuroticism) being associated with a 81% decrease in the rate of
495emigration. These effects were consistent in their direction (though not their
496significance level) in all multi-variable models tested. There was no significant effect
497of “percent time playing” on emigration age in the full model, or in any other model
498tested.

499 Because breeding males (i.e. fathers) are typically the alpha males, and alpha
500males are usually (though not always) evicted during alpha male turnovers, father
501co-residence and the number of alpha male turnovers were negatively correlated
502with one another ($r = -0.25$). Father co-residence was negatively correlated with

503extraversion ($r = -0.26$) and neuroticism ($r = -0.14$). Higher numbers of alpha
504turnovers were positively associated with greater extraversion ($r = 0.22$) and greater
505neuroticism ($r = 0.31$).

506

507(Table 2a,b and Figure 1 here)

508

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

510

511 For the ten males who were included in these analyses (i.e. had sufficient
512accuracy in age estimates and data on the relevant predictor variables), the mean
513(and median) age of becoming alpha male for the first time was 10.7 ± 1.8 years,
514ranging from 8.2 to 14.6 years. Figure 2 shows, for those males with sufficiently
515accurate data on the timing of emigration age and first rise to alpha status, the
516timing of both of these events. Extraversion (Fig. 3) was the only variable that
517emerged as significant in any of our models, with more extraverted males acquiring
518alpha status significantly earlier in life in all models; the effect of extraversion was
519independent of emigration age. Father presence and time spent playing were non-
520significant in all models and also inconsistent in the direction of their effects. Males
521who emigrated later in life also became alpha males later in life, though these effects
522were non-significant. Males who were more neurotic were slightly more likely to
523become alpha males sooner, but this effect was not significant in any of the models
524either. Table 3a shows the results of the models that had a single predictor variable.
525The model in which father presence was the predictor variable violated the

526assumptions of the proportional hazards test and is not presented here, but it was
527clearly not significant ($P=0.74$). Table 3b shows the best fit multivariate model,
528which includes extraversion, neuroticism and emigration age.

529

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

531

532**Discussion:**

533

534It has been well established that the most effective route to achieving reproductive
535success for a male capuchin monkey is to become the alpha male of a group in which
536there are large numbers of females who are not closely related to him (Perry, 2012).

537Thus, the best strategy for achieving high lifetime RS is likely to be to acquire the
538alpha position as early as possible and to retain it for as long as possible, preferably
539in a group composed of unrelated females. This paper examines the factors that are
540associated with earlier natal emigration and rapid acquisition of alpha status.

541

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

543

544 We had expected that more extraverted males would be less fearful of
545striking out on their own and exploring new groups, and hence would emigrate
546sooner than more introverted monkeys. Contrary to our predictions, more
547extraverted males stayed in their natal groups longer. It is not clear to us by what
548mechanism this occurs. Perhaps males who are more extraverted feel more

549 comfortable with the social environment in their natal group (e.g. because they have
550 more playmates and better relationships with potential mates), and therefore feel
551 less compelled to leave. In the future, when we have a larger behavioral data set to
552 work with, we will test whether more extraverted males are also better at attaining
553 higher rank, developing alliances, and attaining more breeding opportunities in the
554 natal group. More neurotic males were also more likely to emigrate later. One
555 possible explanation is that more neurotic males defer emigration because they are
556 more anxious about leaving home and about developing relationships with new
557 monkeys; this would be a rational fear, given the high frequency with which
558 dispersing males are wounded.

559 Males were more likely to stay longer in the natal group if their father stayed
560 longer, and they were more likely to leave early if their early life was characterized
561 by more frequent alpha male turnovers. Because alpha males father most of the
562 offspring, an alpha male turnover generally means eviction of the father of most of
563 the young males. These results are consistent with what we know from the Santa
564 Rosa population of white-faced capuchins. There, the best predictor of age at
565 dispersal is the length of time that a male has co-resided with the male who was
566 alpha at the time of his conception (i.e. the probable father, though genetic paternity
567 was not known in that data set); this variable explained 15% of the variance in their
568 model, but was nonsignificant when one outlier was removed (Jack et al., 2011). At
569 Santa Rosa, natal dispersal was 18.7 times more likely to occur in the aftermath of an
570 alpha male turnover than at other times (Jack et al., 2011). At Lomas, the bonds
571 between fathers and their sons are often strong, particularly once the sons are old

572 enough to participate in intergroup encounters. We have even seen sons co-emigrate
573 with their father after the father is deposed from the alpha position. It is not clear
574 whether the association between paternal co-residence and timing of natal dispersal
575 is due to the strength of the father-son bonds, or to persecution of natal males by
576 immigrant males who attain alpha rank. It has been suggested (Fedigan & Jack,
577 2004) that the risk of being killed by the new alpha and his allies is too great to
578 permit resident males to remain as subordinates at Santa Rosa. At Lomas, for
579 reasons that are not yet clear, we see more cases of incomplete male replacement
580 following takeover events (i.e. more cases in which some subset of the natal and
581 other resident males remain in the group after an alpha replacement from the
582 outside) than are seen in the Santa Rosa population. Further analysis would be
583 required to determine the mechanisms by which males decide whether to stay or
584 leave in the aftermath of a takeover.

585

586 *What factors hasten the initial rise to alpha status?*

587

588 The most consistent effect to emerge from this set of analyses was that more
589 extraverted males attained alpha status sooner; this was a significant effect in all
590 models. It is easy to see how extraversion might enhance ability to become alpha, as
591 a more self-confident and social male might be less inhibited about challenging a
592 higher-ranking animal, and indeed all of the traits that loaded positively on
593 Extraversion (see Material and methods) are traits typically associated with
594 leadership roles. Our analysis of personality (Manson & Perry, 2013) revealed that

595the capuchin variety of extraversion is not the same thing as playfulness, and
596extraversion also had an impact on age of becoming alpha even when controlling for
597the variable “percent time spent playing.” Neuroticism had a nonsignificant tendency
598to hasten rise to alpha status in all of the multivariate models in which it was
599included and always had a much smaller effect size than extraversion. It is not clear
600how neuroticism might help, as many of the contributing traits (e.g. reactivity,
601intolerance/irritability, impulsivity) seem inconsistent with a successful political
602strategy. Aggressiveness (a trait that loads heavily on both extraversion and
603neuroticism) seems consistent with early rise to alpha status, and it is possible that
604the remaining traits associated with capuchin neuroticism – alertness and
605tension/anxiety – might contribute to productive vigilance about monitoring the
606social environment, which might help males gather information regarding the best
607timing for staging a takeover event.

608 There are very few studies demonstrating a link between play in juveniles
609and dominance rank later in life. However, a study of yellow-bellied marmots has
610demonstrated a link between play outcomes in pups and dominance rank as
611yearlings, which attenuates over time (so that the association almost vanishes by the
612time they are adults) (Blumstein et al., 2013). The precise mechanism by which play
613predicts later rank is as yet unknown. Brown bear cubs who play more have a
614greater chance of survival to independence (Fagan & Fagan, 2009), though the
615mechanism by which this occurs is unclear as well. Play probably develops fighting
616skills by improving motor control and neural connections (Bekoff, 1988; Byers &
617Walker, 1995; Bell et al., 2010; Pellis et al., 2010) (but see (Sharpe, 2005b) for an

618 example of how meerkat play does NOT improve fighting skills). Play has also been
619 hypothesized to improve social competence (Pellis et al., 2010), emotional flexibility
620 (Fagen & Fagen, 2009), ability to manipulate others (Brueggeman, 1978),
621 assessment of conspecifics (Pellis & Pellis, 1996), and skills in coping with novel,
622 unexpected situations (Spinka et al., 2001). Many have hypothesized that play
623 solidifies social bonds (Baldwin & Baldwin, 1974; Poirier & Smith, 1974; Palagi,
624 2006). It should be noted, however, that no association between play frequency,
625 social cohesion and co-dispersal was observed in meerkats, the only species in
626 which these ideas have been rigorously tested (Sharpe, 2005a; Sharpe, 2005c).

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

638 Emigration age did not significantly impact the absolute age at which males
639 became alpha for the first time. Visual inspection of this small data set hints at a
640 non-linear relationship between these variables, with really early emigrants and

641really late emigrants taking longer to become alpha males than the males who
642emigrate closer to the median emigration age, but we do not yet have a large enough
643sample size of accurate data points to accurately model age as a non-linear
644relationship.

645 This data set, though quite large by field primatology standards, is still small
646enough that we can expect some fluctuations in the relationship between variables
647in the future as we continue to increase the sample size, particularly given the
648currently high ratio of variables to data points. Sometimes predictor variables are
649not significant when tested singly, but become significant in the context of a
650multivariable model. The multivariable models are necessary to control for the
651effects of other variables; however, the sample sizes are much reduced in the
652multivariable models, due to the necessity of measuring all variables for each male,
653so it may not always be the case that the multivariable models produce a clearer
654understanding of the impact of each variable. This is particularly true for the
655variable “play,” which drops from a sample of N=109 in the single variable model to
656N=33 in some multivariable models.

657

658*Future directions:*

659

660Several interesting questions about males’ early careers remain to be resolved, due
661to lack of sufficient data and due to the analytical challenges of trying to understand
662the interplay between many variables in a dynamic system. Although this is a large
663data set by primatological standards, it is nonetheless the case that a large

664proportion of the life histories documented here remain incomplete even after 25
665years of observation, leaving us with small sample sizes of individuals for which all
666variables can be measured. Ideally, we would want to know the impact of the
667variables measured in this paper on lifetime reproductive success, but the number of
668males for whom we have such information is still too small to warrant quantitative
669analysis. We would also like to know not only the onset of alpha status, but the
670proportion of the entire lifespan spent as alpha male, and the influence of
671personality and early play experience on the ability to prolong time spent as alpha
672male. The lack of influence of play on the timing of emigration and rise to alpha
673status was puzzling, but it may turn out that play impacts males' success in different
674ways. For example, when we have larger data sets on rare events such as
675coalitionary lethal aggression and severe wounds, we will be able to test whether
676play experience in the natal group better prepares males to migrate into a new
677group without incurring major injuries that lead to physical handicaps or death.

678 Additional data will help clarify the costs and benefits of different personality
679types. It has been suggested that selection maintains a variety of personality types
680because they have different fitness consequences in different environments (Penke
681et al., 2007). Alternatively, perhaps personality traits that exert a positive effect on
682fitness during one phase of life exert a negative effect at other points in the
683individual's life history; e.g. life history tradeoffs between early and late
684reproduction result in polymorphisms with regard to strategies of risk aversion
685(Wolf et al., 2007). Extraversion appears to give white-faced capuchin males an
686advantage in attaining alpha status early in life; but if we continue to study these

687monkeys for longer, will we discover negative effects of extraversion, such as
688increased risk of early mortality due to boldness in combatting conspecific rivals or
689predators? Neuroticism seems to be particularly promising as a trait that is likely to
690be beneficial in some situations and costly in others. Further investigation of the
691relationship between personality traits and fitness-relevant decisions that animals
692make is likely to clarify aspects of the debate about why a diversity of animal
693personalities has evolved.

694

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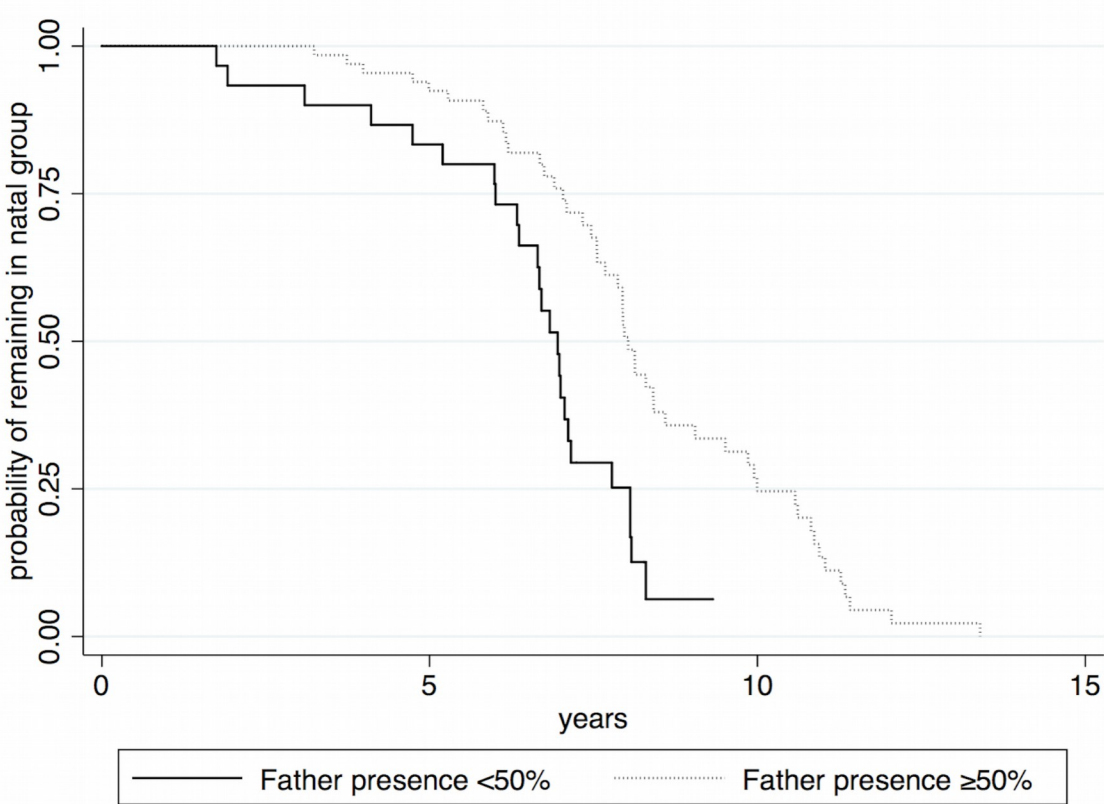
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914**Figures:**

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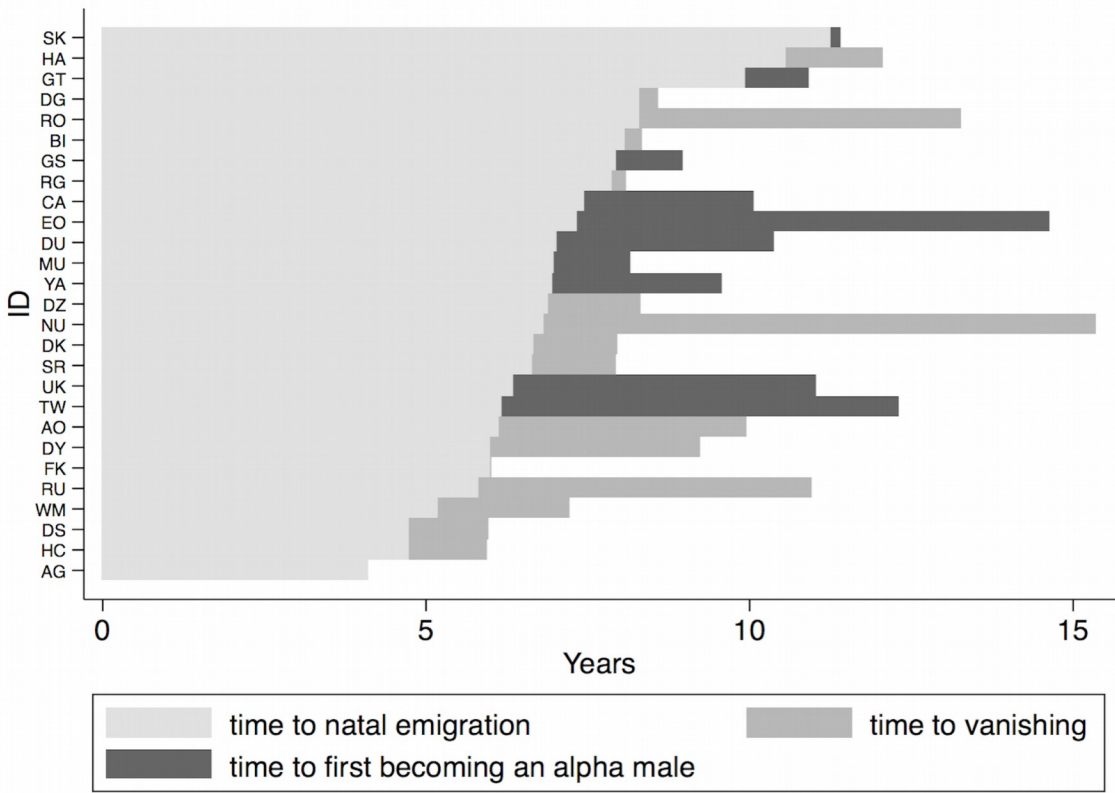
916Fig. 1: Kaplan-Meier survival estimates for the effects of father presence on
917emigration age. The solid line shows the population for which the father was present
918>50% of the first 5 years of the male's life and the dotted line shows the population
919for which the father was present <50% of the male's first 5 years of life. The X-axis
920represents the time since the males' birth in years, and the Y-axis represents
921cumulative probability of survival.



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

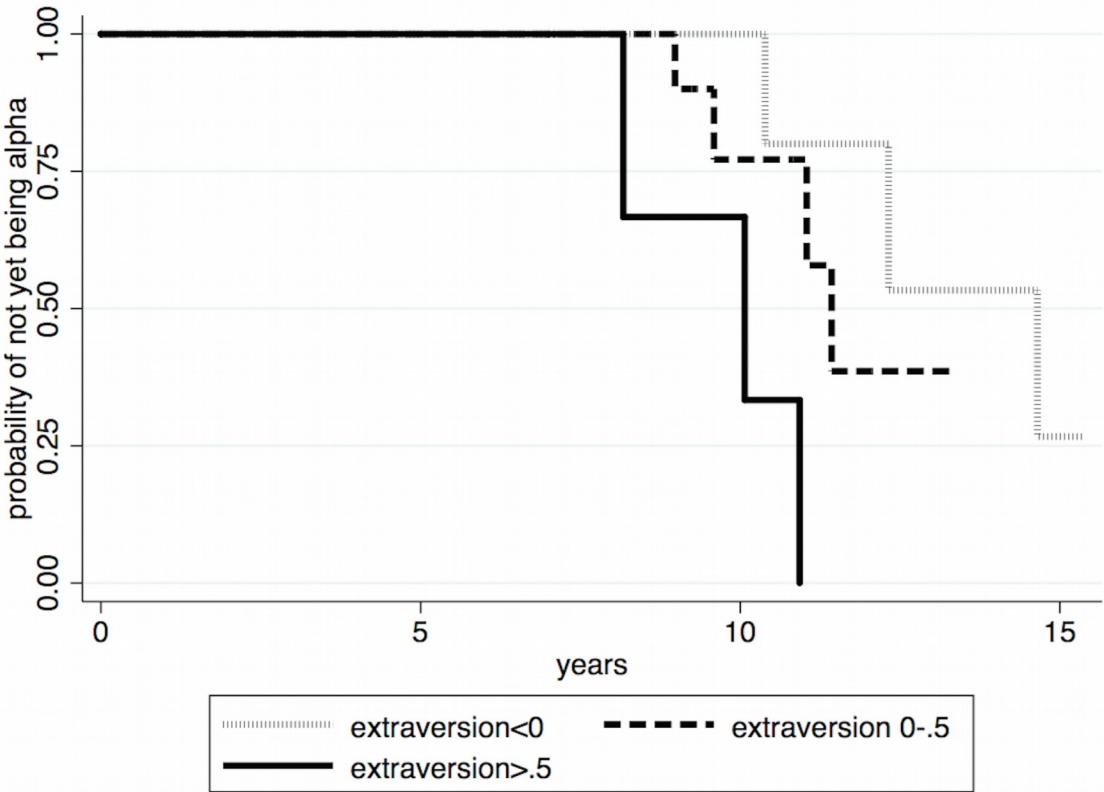


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932 Fig. 3: Kaplan-Meier survival estimates for the effects of extraversion on the age at
933 which males acquire alpha status for the first time. The X-axis represents the time in
934 years, and the Y-axis represents cumulative probability of survival.

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938 Table 1: Sample sizes and distributions of variables used in each analysis.
 939

	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
				28.5	
Percent Play	6.60	3.34	1.35	7	109
	66.5	36.8			
Father presence (%)	1	6	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
				14.3	
Percent Play	7.10	2.45	1.35	4	38
	63.4				
Father presence (%)	4	37.67	0	100	38
Age of Becoming Alpha, Single Variable Analyses					
				11.2	
Age of emigration	6.37	2.3	1.19	7	53
Extraversion	0.13	0.34	-0.61	0.84	40
Neuroticism	-0.04	0.37	-0.82	0.81	40
				28.5	
Percent Play	6.44	3.38	1.35	7	109
Father presence (%)	64.7	37.39	0	100	71
Age of Becoming Alpha, Multiple Variable Analyses					
				11.2	
Age of emigration	7.20	1.83	3.99	7	33
Extraversion	0.14	0.37	-0.61	0.84	33
Neuroticism	-0.05	0.32	-0.76	0.81	33
				14.3	
Percent Play	7.23	2.23	3.24	4	33
	62.4	38.0			
Father presence (%)	0	1	0	100	33

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944 Table 2a: Single predictor variable models in which the outcome variable is age of
 945 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	0.00	0.015	0.984 to 0.998	70
		4			
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

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

949

Predictor variable	Hazard ratio	SE	P	CI
# alpha turnovers	1.05	0.02	0.029	1.00 to 1.09
Father presence	0.989	0.00	0.024	0.979 to 0.999
		5		
Extraversion	0.28	0.15	0.017	0.099 to 0.793
Neuroticism	0.20	0.14	0.018	0.054 to 0.758

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

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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

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

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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

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