Male residency and dispersal triggers in a seasonal breeder with influential females

Christopher Young[a,b,c], Richard McFarland[d,e], Andre Ganswindt[a], Mirjam M.I. Young [b,f,g], Louise Barrett[b,c], and S. Peter Henzi[b,c]

[a]Endocrine Research Laboratory, Mammal Research Institute, Faculty of Natural and Agricultural Science, University of Pretoria, Pretoria, Republic of South Africa, [b]Applied Behavioural Ecology and Ecosystems Research Unit, University of South Africa, Florida, Gauteng, South Africa, [c]Department of Psychology, University of Lethbridge, Lethbridge, Alberta, Canada, [d]Department of Anthropology, University of Wisconsin-Madison, Madison, United States, [e]Brain Function Research Group, School of Physiology, University of the Witwatersrand, South Africa, [f]Behavioural Ecology, University of Leipzig, Germany, [g]Research Group Primate Kin Selection, Max-Planck-Institute for Evolutionary Anthropology

Corresponding authors address: *Endocrine Research Laboratory, Mammal Research Institute, Faculty of Natural and Agricultural Science, University of Pretoria, Pretoria, Republic of South Africa*

Email: Christopher.young@uleth.ca

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ABSTRACT

Males in female-philopatric social groupings leave their natal groups in order to pursue successive reproductive opportunities in one or more subsequent groups. In vervet monkeys (*Chlorocebus pygerythrus*), adult males coexist, and physical eviction is not a driver of male movement. Migratory decisions are expected to turn on an evaluation of future reproductive opportunity, as indexed principally by local operational sex ratio and relative competitive ability. Although vervet males' reproductive success is correlated with dominance, they are distinctive in that the attainment of rank is contingent on integration into female socio-spatial networks and we expect decisions about continued residency to reflect this. We used eight years' data from three groups to confirm that male dispersal between groups is seasonal in our population, with a peak that is coterminous with androgen levels, and precedes peak mating and conception by four weeks. The average length of completed residency was 459.00 days (± 509.85 SD; Median=400.50), with an increase in the logged rate of departure after 1428 days, which is 150 days longer than the estimated modal age at first conception by putative daughters. There were positive correlations between a male's initial and highest rank, and between his highest rank and the length of time to reach it. We found that a male's residency was positively and independently associated with his highest achieved rank and both his grooming centrality and proximity degree. Additionally, increasing rank and proximity degree also had positive effects on residency length subsequent to the attainment of his highest rank. The probability of emigration was associated negatively with both female number and grooming centrality scores. We conclude that emigration from a group is linked to male rank attainment and mediated by a male's integration into female socio-spatial networks. We found no evidence that emigration preceded the sexual maturity of putative daughters.

Keywords: *Chlorocebus pygerythrus*; dominance; group residency; male dispersal; social integration; tenure length.

INTRODUCTION

Inbreeding avoidance and maximisation of lifetime reproductive success are the two main drivers of dispersal from the natal group and subsequent, secondary inter-group movement for males in gregarious mammalian social systems (Greenwood, 1980; Pusey and Packer, 1987). At the same time, competition for access to mates is a defining characteristic of mammalian male social life. Where males co-reside in groups (multimale social systems), and other groups are accessible, the duration of a male's tenure in a group is set principally by his local competitive ability (Clarke *et al.*, 2008) and the availability of sexual partners, and circumscribed by the increasing probability of residing alongside reproductively mature female offspring (Henzi and Lucas, 1980; van Noordwijk and van Schaik, 2004).

Where a male's reproductive opportunities are positively tied to his individual dominance rank – which characterises many primate social organisations (Schülke and Ostner, 2012) – competitive ability is generally assessed in these terms alone. However, in many species, dominance-based reproductive advantages can be circumvented by, for example, coalition formation among males (Bercovitch, 1988; Noë and Sluijter, 1995; Young *et al.*, 2013), or the ability of females to choose their sexual partners (see, for example, Dubuc *et al.*, 2011; Young *et al.*, 2013). Vervet monkeys (*Chlorocebus pygerythrus*) present an interesting intersection of these routes to male reproductive success. While males do form coalitions, these appear to have little impact on mating access (Freeman *et al.*, 2016), and there is a positive correlation between rank and both mating opportunities (Freeman *et al.*, 2016) and paternity (Minkner *et al.*, 2018). At the same time, however, we have shown that, in addition to any agonistic efforts on his own behalf, improvement in a male's rank—and therefore in his reproductive opportunities—is tied to the extent to which he is socially and spatially integrated in the female network, indicating an additional, indirect role for the expression of female choice (Young *et al.*, 2017a, see also Raleigh and McGuire, 1989). The fact that vervet males rise in rank relatively slowly during their tenure (see below) also points to a need to cultivate relationships with females and suggests that relevant social factors will therefore also factor into decisions about tenure and the timing of dispersal in this species.

We take advantage of a data set spanning eight years and three large social groups to consider the factors that influence group residency length in male vervet monkeys, and the factors that may trigger a male's decision to leave their current group. Vervet females are philopatric and males leave their natal groups to commence their reproductive careers in other groups, from which they will subsequently also emigrate, with little time spent outside of a group (Henzi and Lucas, 1980). After confirming that male dispersal maps broadly onto the mating season at our site, being most closely prefigured by increases in androgen levels - so demonstrating that the decision to leave a group is concordant with the pursuit of reproductive interests - we first assess the extent to which the duration of a male's residence in any one group is tied to the attainment of rank. While the achievement of a particular rank rests, in part, on a male's intrinsic physical condition, females also have an important and persistent role to play (Young *et al.*, 2017a). We predict, therefore, that the extent of rank improvement will be positively correlated with residency length, as males construct and develop important relationships with females. If this is so, we also predict positive correlations between the highest rank achieved, the extent of socio-spatial integration, and the length of residency after the achievement of this rank. Clearly, a male who is high ranking would be expected to capitalise on his dominance status, while one that is socially integrated might justifiably expect further rank improvement, even if this does not materialise.

We then examine the possible factors that trigger a male's decision to leave a group. In addition to a male's mating success in the previous mating season and unfavourable shifts in the operational sex ratio (more males, fewer reproductively active females), we expect declines in both rank and socio-spatial integration to increase the likelihood of departure to another group. In this vein, we also use a much larger data set, a more accurate estimate of female sexual maturity (3.5 years or 1278 days), and a more appropriate analytical approach, to revisit an earlier proposition that vervet male residency has an upper limit that is set by the modal age at which putative daughters begin reproducing, and is thus geared to lower the risk of inbreeding (Henzi and Lucas, 1980).

METHODS

Study site and subjects

Our research was conducted at the Samara Private Game Reserve, in the Eastern Cape, South Africa (32°22'S, 24°52'E). We collected data on three groups (PT, RBM, RST) of wild vervet monkeys, occupying a semi-arid Karoo, riverine woodland habitat (Pasternak *et al.*, 2013). All animals were fully habituated and individually identifiable. Data presented here were collected between September 2009 and December 2016. Group composition varied across the three groups and the study period ($N_{\text{Males:}}$ RBM = 4-19, RST = 5-19 and PT = 3-12. N_{Females} RBM = 7-17, RST = 11-22 and PT = 8-11). Each group was followed for 10 hours per day. Due to variation in the length of daylight hours across the year, we balanced our daily follows in summer so that there were equal numbers of days that began at dawn and finished 10 hours later and days that began later and ended at dusk. In winter, daylight hours (07:30-17.30) generally coincided with our sampling period.

Behavioural data collection

Behavioural data were collected via scan sampling (Altmann, 1974). We conducted scan samples every 30 minutes for a duration of 10 minutes per scan sample throughout the day. During each scan we recorded the general activity of each adult individual (resting, moving, foraging or allo-grooming), as well as the identity of all its nearest neighbours within a 2 m radius (N = 493,756 scans; McFarland *et al.*, 2015; Pasternak *et al.*, 2013). We recorded the identity of each grooming partner and whether the individual being scanned was giving or receiving grooming. We controlled for observer effort (number of observers/group/scan day; range: 1-3), and for the presence of each individual on each scan day (based on daily group census). Agonistic behaviours were recorded *ad libitum.*

Dominance rankings and power trajectories

Our study was divided into three-month blocks fixed by the mating (April-June) and birth seasons (October-December), separated by the January-March and July-September periods. Male-male dominance hierarchies were constructed separately for each three-month period and each group from decided agonistic interactions ($N = 5{,}212$). We constructed three-month winner-loser matrices for each group and entered these into the excel macro from the "DomiCalc" package (Schmid and de Vries, 2013), allowing us to calculate standardized normalized David's scores (SDS). We standardized our dominance ranks by dividing each individual's David's score by the maximum value for that time period and group (Henzi *et al.*, 2013). This gave the highest-ranking individual for each group and time period a score of one and allowed us to generate comparable rank scores across groups and time periods. Using decided dyadic agonism, we determined the level of aggression each male received from females over each 3-month block. The visibility of the habitat and the modal presence of more than one observer gives us confidence that there was no systematic bias in the recording of agonism. Only individuals present during each three-month period were included in each matrix (calculated from daily census data).

We estimated each male's power trajectory by determining Elo-ratings (Albers and de Vries, 2001; Neumann *et al.*, 2011), using the R package "EloRating" (Neumann *et al.*, 2011) and the function "traj.elo". For a full description of the method see Young et al. (Young *et al.*, 2017a). In brief, a male's Elo scores at the start and end of each three-month period were used to describe his power trajectory, expressed as the slope of the line connecting them. Positive and negative slopes indicate increasing and decreasing power within the group respectively, while the magnitude of the slope identifies the rate of increase or decrease. In order to provide a stable baseline for the Elo ratings we used the 3-month period prior to the beginning of analyses, i.e., between September and December 2009 to generate each males' initial rating. The number of points that can be won or lost is determined by the k value, which we set to the recommended moderate level of 100 (Neumann *et al.*, 2011).

Social indices

For non-human primates, social relationships are constructed and maintained via affiliative behaviours, and repeated measures of affiliative behaviours over time can provide a proxy for individual social relationships within a group (such as grooming or being in social proximity) (Hinde, 1983). We used our scan data to examine vervet monkey social relationships. To do so, for each three-month period and group, we constructed spatial (<2 m) and allo-grooming association matrices. We controlled for observation effort by dividing each dyadic association score by the total number of scans in which each dyad was observed during each period, and the number of weeks during which each individual of the dyad was observed in the group in each period. As we were interested in a male's social integration into the whole group, we examined all adult social relationships when constructing our social networks. For our vervet population two social network (SN) measures have been shown to be important (Josephs *et al.*, 2016; McFarland *et al.*, 2015; Young *et al.*, 2017a). These are 1) grooming Eigenvector Centrality (EC), a measure of how connected (central) each male is in the group in relation to how connected his partners are. That is, it is an estimate of how socially integrated an individual is in the grooming network. 2) Proximity Degree, a measure of the number of different nearest neighbours with which an individual is associated. In line with Castles *et al.* (2014), we examine grooming and proximity metrics separately.

Mating and conception

We used observed mating as our index of reproductive access (Freeman *et al.*, 2016). We recorded all observed copulations between males and females on our three groups *ad libitum*. As for scan data, we are confident that there are no systematic biases in the records. For each mating season we determined the number of copulations for each male. We divided this score by the total number of copulations for that group and year to give the proportion of all copulations each male received each year. Female conception date was calculated from the date of birth of an infant using a gestation estimate of 165 days.

Residency length

We determined group residency length for each individual male as the total time in days that a male was scored as present in a group and was recorded in scan samples. Groups were followed on a near daily basis; occasionally, however, a male emigrated when we were not in the field. If so, the day that was at the midpoint between the two consecutive observation days was allocated as the day of dispersal.

Androgen metabolite levels

Faecal samples for steroid analyses were collected from all adult males on a bi-monthly basis as part of a long-term project investigating vervet monkey physiological stress. In order to identify the possible shift in androgen production from pre-mating to mating season, as an exploratory assessment of the role of intrinsic dispersal triggers to complement data on extrinsic factors such as mating activity, we selected five males, analysing one sample from each over the period Jan – May 2016, which covers the period before and after peak migration. This gave a total of five samples per male. The faecal sample collection and processing used standardized protocols for both the field and the laboratory and are described in Young et al. (2017b). Steroid extractions, as well as, enzyme immunoassays (EIA) were conducted at the Endocrine Research Laboratory, University of Pretoria. Steroids that had previously been extracted for faecal glucocorticoid metabolite analysis were stored in a freezer at the Endocrine Research Laboratory were used for this study (for details see Young *et al.*, 2017a). We examined androgen production via quantification of immunoreactive faecal androgen metabolites (fAM) using a T-3-CMO EIA. Details of the EIA, including cross-reactivities of the antibody used, are described by Palme and Möstl (1993) and all steroid concentrations are given as ng/g faecal dry weight (DW). The EIA was performed using a standardized protocol (see Ganswindt *et al.*, 2002) and biologically validated for the species by contrasting fAM concentrations of sexually mature ($N = 5$; mean ± SD: 592.80 ± 263.17 ng/g DW) and immature ($N = 9$; mean ± SD: 223.95 ± 78.08 ng/g DW) males ($T = 57$; $P = 0.011$). The sensitivity of the EIA used was 2.4 ng/g faecal DW. Intra- and Inter-assay coefficients of variation, of high- and low- value quality controls, were 4.7% and 6.2% as well as 8.8% and 12.7%, respectively.

Statistical analysis

With the exception of the assessment of the distribution of male probability of departure, all statistical analyses were run in R 3.5.2. (R-Core-Team, 2018)

We used a Rao spacing test to examine if the observed number of migrations per month varied from that of uniform distribution using the r package “circular” (Agostinelli and Lund, 2011). To describe the relationship between the timing of male inter-group movement, mating and conceptions, we used the "forecast" package in R (Hyndman and Khandakar, 2008) to identify the lag in weeks at which the respective cross-correlations were highest.

Using data only from non-natal males, we first determined whether the probability of male departure was independent of the duration of his residency (i.e., whether the “failure” rate was constant), by fitting the data to an exponential distribution in JMP 13 (JMP, 2013). Following visual examination of the fit, we used the ‘survival’ platform in JMP to derive estimates of survival that accounted for censored data. We then used the "segmented" package in R (Vito, 2008) to establish whether the regression between log survival and residency length was the best fit by separate line segments. Breakpoints were evaluated by checking the corresponding gap coefficient and its *t*-value, (breakpoint accepted when $t<2.0$).

We ran a time-dependent cox proportional hazards model (Mills, 2011; Therneau and Grambsch, 2013), using the “coxme” package (Therneau and Therneau, 2015) to examine the influence of social network position and SDS on male residency length (model 1). We included residency length in days as our time series along with three predictor variables: 1) a male’s highest rank position, 2) his highest grooming EC score and, 3) his highest proximity degree score.

We ran a second survival analysis using a cox proportional hazards model in order to investigate if male residency length subsequent to achieving their top rank position was predicted by their social network position and their highest rank position (model 2). We specified group residency length subsequent to achieving top rank as the response variable and included the following predictor variables: 1) highest SDS; 2) highest grooming EC score; 3) highest proximity degree score and, 4) residency length prior to achieving their highest rank as a statistical control.

We then ran a third cox regression model (model 3) with time-varying covariates (Mills, 2011; Therneau and Grambsch, 2013) to examine the influence of the predicted time-varying factors on a male's decision to leave. We split each male's tenure into three-month blocks with the male's status at the end of each three-month block being stay or migrate (binary: 0/1) from the group, this gave 37 known migratory events, and 386 three-month blocks from 56 males (19 males with censored data; seven migratory events and 12 censored males could not be included in this analysis as these males stayed for three months or less and differences in social metrics between two periods could not be calculated). This allowed us to test a number of time-varying and binary covariates using the function "coxme" to allow for random effects. If a male migrated after one month or less in a time block, we used the previous time period as his last time block to determine our dependent variables, as periods of less than one month are too short for data to be reliable. All numeric predictor variables were standardized to provide a mean of 0 and standard deviation (SD) of 1. Our predictor variables were: 1) the difference in value of a male's SN measures from the beginning to the end of a three-month block for proximity degree and grooming EC, 2) the difference in SDS from the beginning to the end of a three-month block, 3) a male's power trajectory, 4) a male's mating success during the previous mating season, 5) the proportion of female group members with dependent infants and, 6) the number of adult females in the group.

We incorporated right-censored data in all the cox regressions to account for animals that had not yet left the group at the end of the study period, and we included only individuals who were observed to have transferred to one of the study groups or three semi-habituated neighbouring groups (i.e. not individuals that might have died rather than migrated). For all models we included individual identity nested within group as a random effect as well as random slopes for the grooming EC variable in model 3.

In order to check the validity of our cox models we examined the Cox-Snell residuals, scaled Schoenfeld residuals using the function "cox.zph" in the R package "survival" (Therneau, 2014) and, for influential cases, used df beta to look at score residuals (Mills, 2011; Therneau and Grambsch, 2013). Using the function "vif" from R package "car" (Fox and Weisberg, 2011), we examined variance inflation factors (VIFs) derived from linear (models 1 and 2) and binomial (model 3) models containing all predictor variables to assess collinearity. All VIFs were < 2, indicating that collinearity was not an issue (Pan and Jackson, 2008; Field *et al.*, 2012). We used the 'MuMIn' package (Barton and Barton, 2015) to generate marginal and conditional R^2 values for the whole models using the function "r.squaredLR" (Nakagawa and Schielzeth, 2012).

To examine if there was a difference in the length of time it took a primary or secondary migrator to achieve their top rank, and to deal with small sample sizes, we ran a Bayesian two sample t-test, using the "bayes.t.test" function from the "Bolstad" package (Curran and Bolstad, 2017).

We follow Colquhoun (2014) in describing outcomes as indicating weak (*P* ~0.05), moderate (*P*~0.01) or strong (*P*~0.001) evidence for effects.

Ethical note: All protocols were non-invasive and adhered to the laws and guidelines of South Africa and Canada. Procedures were approved by the University of Lethbridge Animal Welfare Committee (Protocols 0702 and 1505). This study also adheres to the ASAB/ABS Guidelines for the Use of Animals in Research.

RESULTS

Timing of dispersal

Over the course of the entire study period, 138 males were observed to reside in our study groups. Of these males, 14 are known to have died, 20 males were present at the start of the study (of which 12 had known subsequent emigrations) and 19 males were present at the end of the study period. Of the remaining 90 males, 63 migrated to a new adjacent group, of which 19 were by males leaving their natal groups. Including immigrants of unknown provenance did not affect the outcomes. All known males transferred directly into adjacent groups. Males dispersed most frequently in the months of April and May (45 of 63 migrations) and the annual distribution of dispersal was not uniform (*Rao spacing statistic* = 297.692, $N = 63$, $P < 0.001$). We also recorded six incidents of parallel dispersal, where two males from the same group moved on the same day. These were all natal males moving for the first time and accounted for 19% of the total dispersal events, or 63% of natal dispersal events. We had one observation of a 3-year-old juvenile moving with a 4-year-old and a 5-year-old sub-adult between two of our study groups (all natal males).

There was a correlation between the number of migrations that occurred in a given week of the year and the number of female conceptions in the same week (r = 0.54, $N_{\text{weeks}} = 52$; $N_{\text{conceptions}} = 180$; $N_{\text{migrations}} = 63$, p < 0.001). A similar outcome was found for the number of matings in a given week and the number of males moving in that week (r = 0.57, $N_{\text{matings}} = 353$, p < 0.001). However, the fit between dispersal and both number of female conceptions and matings was improved if matings and conceptions were lagged by 4 weeks (Conceptions: r = 0.810, $N_{\text{weeks}} = 52$, $N_{\text{conceptions}} = 180$, P < 0.001; matings: r = 0.81, $N_{\text{weeks}} = 52$, $N_{\text{matings}} = 353$, $P < 0.001$).

The level of fAM rose from January until April, when they peaked alongside migrations before declining (Figure 1).

What predicts group residency length?

The completed residency length for 44 non-natal males was 459.00 days (± 509.85 SD. Range 31 – 2696 days; Median: 400.50). The duration of non-natal male residency was best described by an exponential distribution (Kolmogarov's D: 0.071; $N = 44$ dispersal events plus 32 censored males; $P = 0.15$), indicating that the overall probability of departure was independent of the duration of residency. Nevertheless, visual examination revealed directional deviations from the fit to the regression at long durations, suggesting the emergence of other processes. This was confirmed by segmented regression, which estimated two breakpoints: one at 1428.13 days (β = -3.36e-04 ± 7.62e-06 SE, t =-44.06), after which the slope was steeper (β = -4.59e-03 ± 2.67e-04 SE, t = -17.23), indicating an accelerating probability of departure, and one at 1529.17 days, after which it was essentially flat (β = -2.93e05 ± 3.07e-05 SE, t =-0.96) and accounted for simply for the persistence of three males

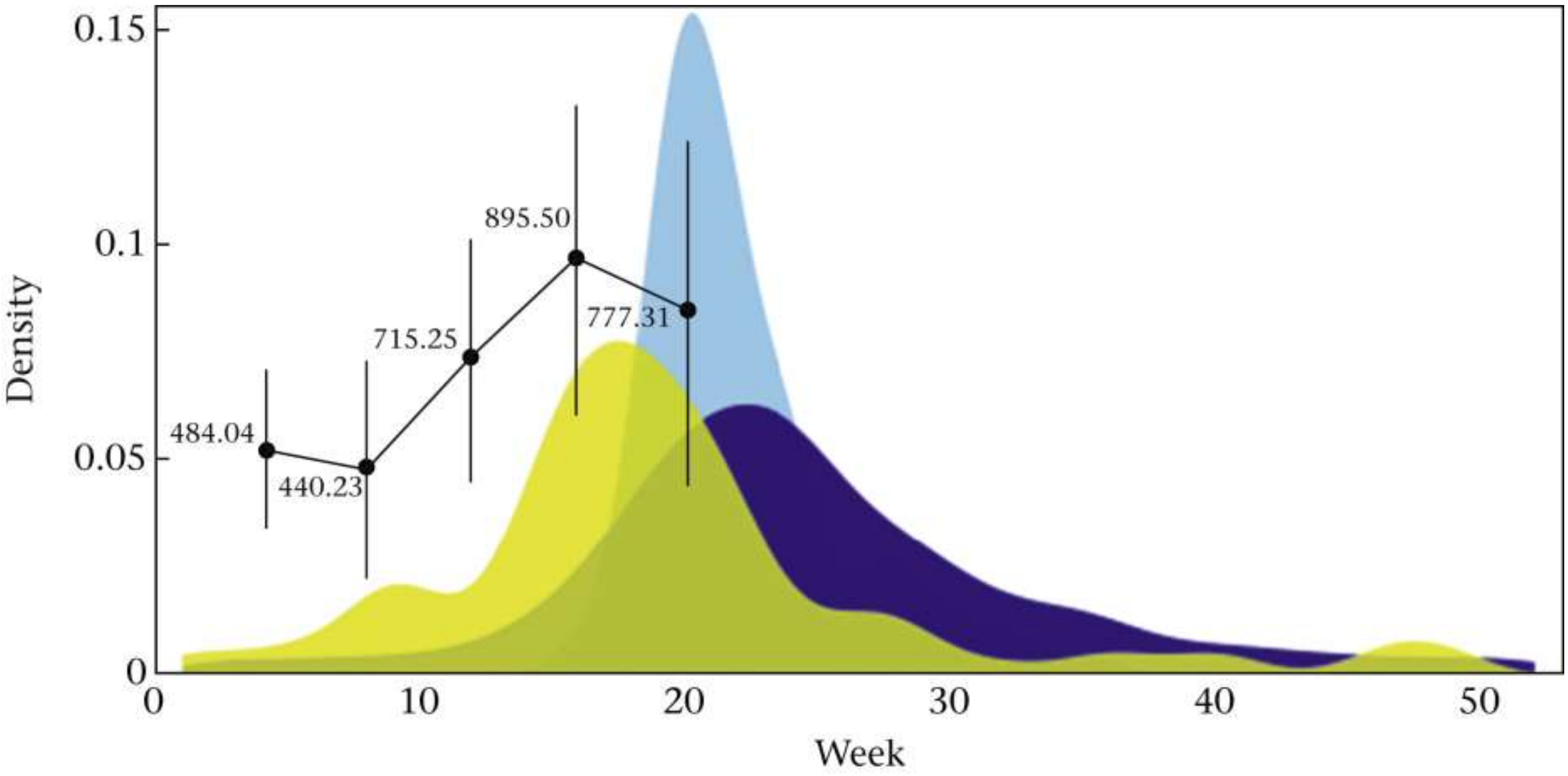

Figure 1. Kernel density estimates of the number of male dispersal events (yellow), together with the number of copulations (dark blue) and the number of conceptions (light blue) per week of the year (1–52 weeks). The mean levels of faecal androgen metabolites (± SD) of five males for the months of January to May illustrate the timing of peak androgen production.

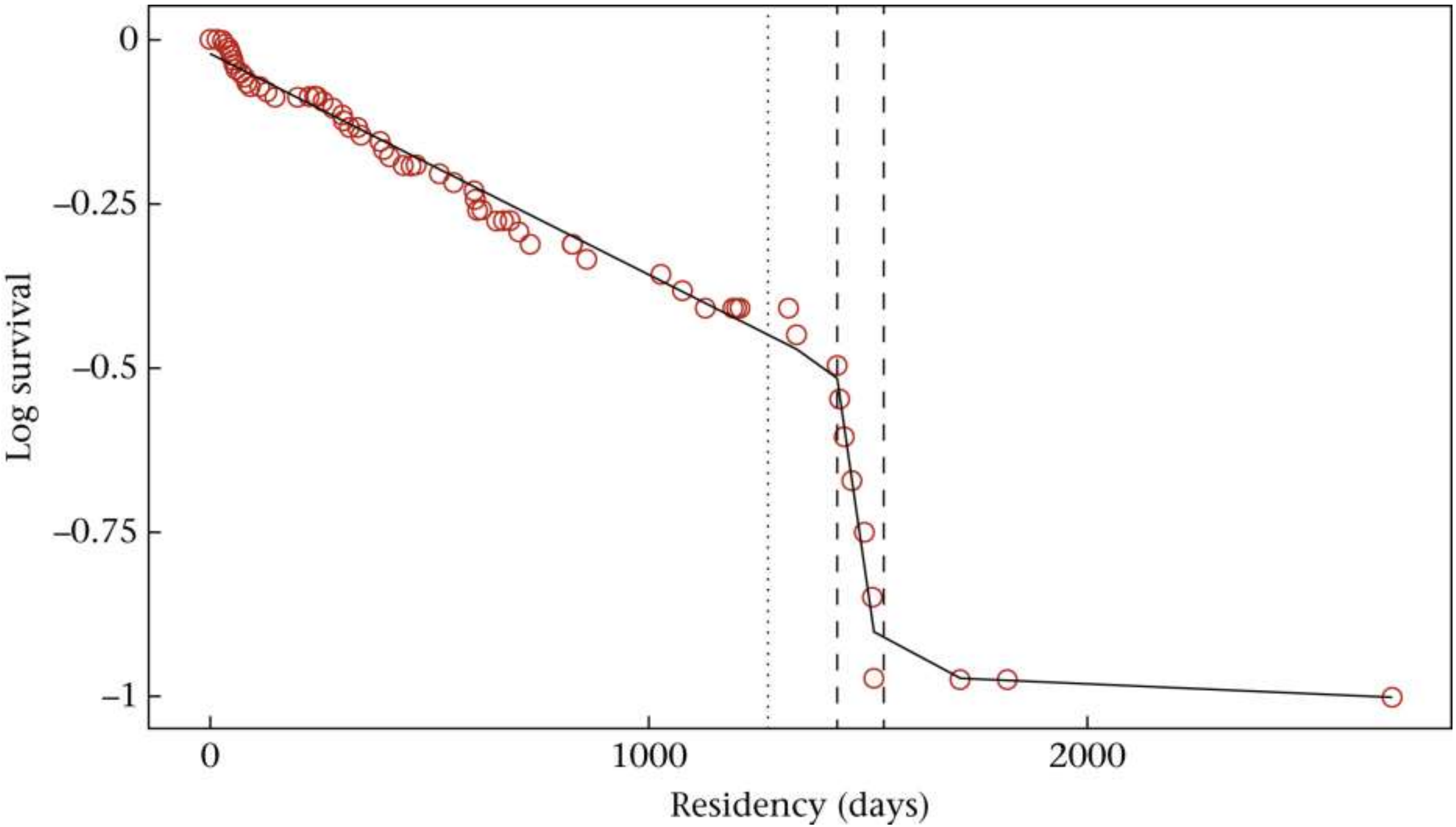

Figure 2. The log-survivorship curve of non-natal males as a function of residency length (red circles). The best-fit segmented regression slopes are fitted as a solid black line ($R^2_{adj.} = 0.99$), and the two identified break points are indicated by dashed lines. The modal age at first birth by females is indicated by the dotted line.

(Figure 2). Given this, we restricted comparison to the first two slopes, and used the "pscore test" function (Vito, 2008) to confirm that they differed (Pscore = -2.877, $P < 0.001$).

There was moderate evidence of a correlation between a male's initial rank on entering a group and the highest rank he achieved in that group (Pearson's r = 0.39, $N = 42$, $P = 0.010$). At the same time, there was strong evidence that the number of days it took a male to reach his highest rank (484.00 ± 403.922, Median = 364 days) was positively correlated with the rank itself (Pearson's r = 0.645, $N = 42$, $P < 0.001$). In this regard, there was a meaningful difference between the time it took for primary (500.13 ± 384.44 days, Median = 356 days) or secondary migrators (261.67 ± 166.41 days, Median = 242 days) to reach their top rank after immigration (Bayes t-test: t = 3.24, df = 16, $P = 0.005$, CI = 134.91 - 646.48 days, $N_{\text{Primary}} = 8$, $N_{\text{Secondary}} = 9$).

We ran a survival analysis (model 1, $N = 44$ migratory events plus 32 censored males) to investigate if male residency length was predicted by rank, grooming EC and proximity degree. The results indicate that our predictor variables had a clear influence on residency and differed from the null model (LR test: $X^2_3 = 60.3$, $P<0.001$). Increases in the rank and proximity variables had strong negative effects on the probability of emigration while there was only very weak evidence for an effect of grooming EC (Table 1). As the highest rank a male achieved increased by one unit, the likelihood of emigration decreased by 67% (hazard ratio = 0.325). Similarly, for proximity degree an increase of 1 unit decreased the likelihood of departure by 56% (hazard ratio = 0.437) and an increase in grooming EC of 1 unit decreased the likelihood of departure by 37% (hazard ratio = 0.625).

Table 1: Output of the cox proportional hazards model to investigate the influence of three social factors on a male's group tenure length (Model 1).

Factor	ß ± se	Hazard ratio	z	Pr(>|z|)
Highest rank a male achieved	-1.124 ± 0.293	0.325	-3.830	<0.001
Highest grooming EC a male achieved	-0.469 ± 0.272	0.625	-1.730	0.084
Highest proximity degree a male achieved	-0.827 ± 0.250	0.437	-3.300	<0.001

N = 44 + 32 censored migratory events. Whole model: log-likelihood = -149.71: $X^2_3 = 60.30$, *P* <0.001; $R^2_{adj} = 0.570$. β is the hazard rate coefficient where a positive value indicates an increased risk of a male dispersal.

We found moderate evidence that the length of a male's tenure subsequent to the achievement of his highest rank was predicted by the highest rank position that he had achieved (model 2, $N = 44$ migratory events plus 19 censored males). With each decrease in rank by one unit, the probability of staying for longer in the group decreased by 63% (hazard ratio = 0.37 table 2; Figure 3). We also found a moderate effect for proximity degree, where a one-unit reduction in degree led to a 69% decrease in the probability of staying longer (hazard ratio = 0.31, table 2). In the aggregate, our predictor variables had a clear influence on residency after achieving top rank and differed from the null model: LR test: $X^2_4 = 24.58$, $P<0.001$).

What factors trigger male dispersal decisions?

We ran a survival analysis to investigate if social factors influenced a male's decision to leave his current group. Overall, the model (model 3, $N = 37$ migratory events plus 19 censored males) showed that changes in our predictor variables influenced the probability of emigration (Table 3. Log-likelihood ratio test comparing the full model to the null model with no predictor variables: $X^2_8 = 15.75$, $P = 0.046$). The model outcomes indicate that the number of females in the group had a weak influence on a male's probability of emigrating, with each increase in female group membership equating to a 41% reduction in the

Table 2: Output of the cox proportional hazards model (Model 2) to investigate the influence of social factors on a male's group tenure length subsequent to achieving his highest rank.

Factor	ß ± se	Hazard ratio	z	Pr(>|z|)
Highest rank achieved	-0.994 ± 0.410	0.370	-2.450	0.014
Highest grooming EC achieved	-0.283 ± 0.400	0.753	-0.710	0.480
Highest proximity degree achieved	-1.184 ± 0.459	0.306	-2.580	0.010
Group residency length prior to highest rank	0.574 ± 0.389	1.775	1.480	0.140

N = 44 + 19 censored migratory events. Whole model: log-likelihood = -140.23: $X^2_4 = 24.58$, *P* <0.001; $R^2_{adj} = 0.341$. β is the hazard rate coefficient where a positive value indicates an increased probability of longer tenure length.

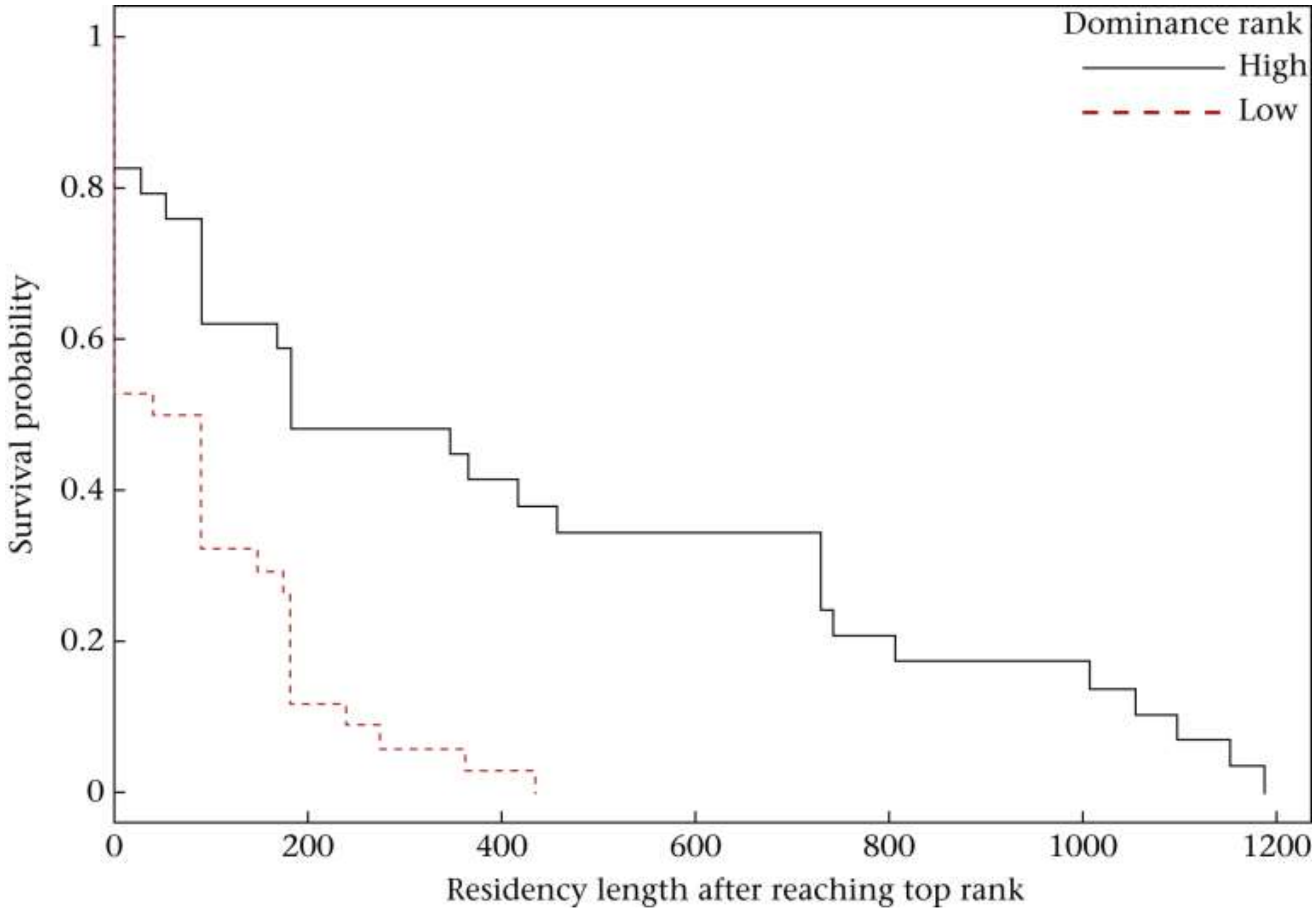

Figure 3. The relationship between rank and male residency length (model 2). In the statistical analysis, male dominance rank is a continuous variable (see Results).

Table 3: Output of the cox proportional hazards model to investigate the influence of several social factors on a male's decision to depart or not.

Factor	β ± se	Hazard ratio	z	Pr(>|z|)
Difference in proximity degree	-0.249 ± 0.182	0.780	-1.370	0.170
Difference in grooming EC	-0.449 ± 0.173	0.638	-2.590	0.001
Standardized rank	-0.034 ± 0.197	0.966	-0.170	0.860
Power trajectory	-0.153 ± 0.156	0.858	-0.980	0.330
Mating success	-0.227 ± 0.214	0.797	-1.060	0.290
Male number	0.299 ± 0.233	1.349	1.280	0.200
Female number	-0.536 ± 0.237	0.585	-2.260	0.024
Proportion of females with dependent infants	-0.212 ± 0.198	0.809	-1.070	0.280

$N = 37 + 19$ censored migratory events Whole model: log-likelihood = -97.617: $X^2_8 = 15.75$, $P = 0.046$, $R^2_{adj} = 0.07$. β is the hazard rate coefficient where a positive value indicates an increased risk of a male dispersal.

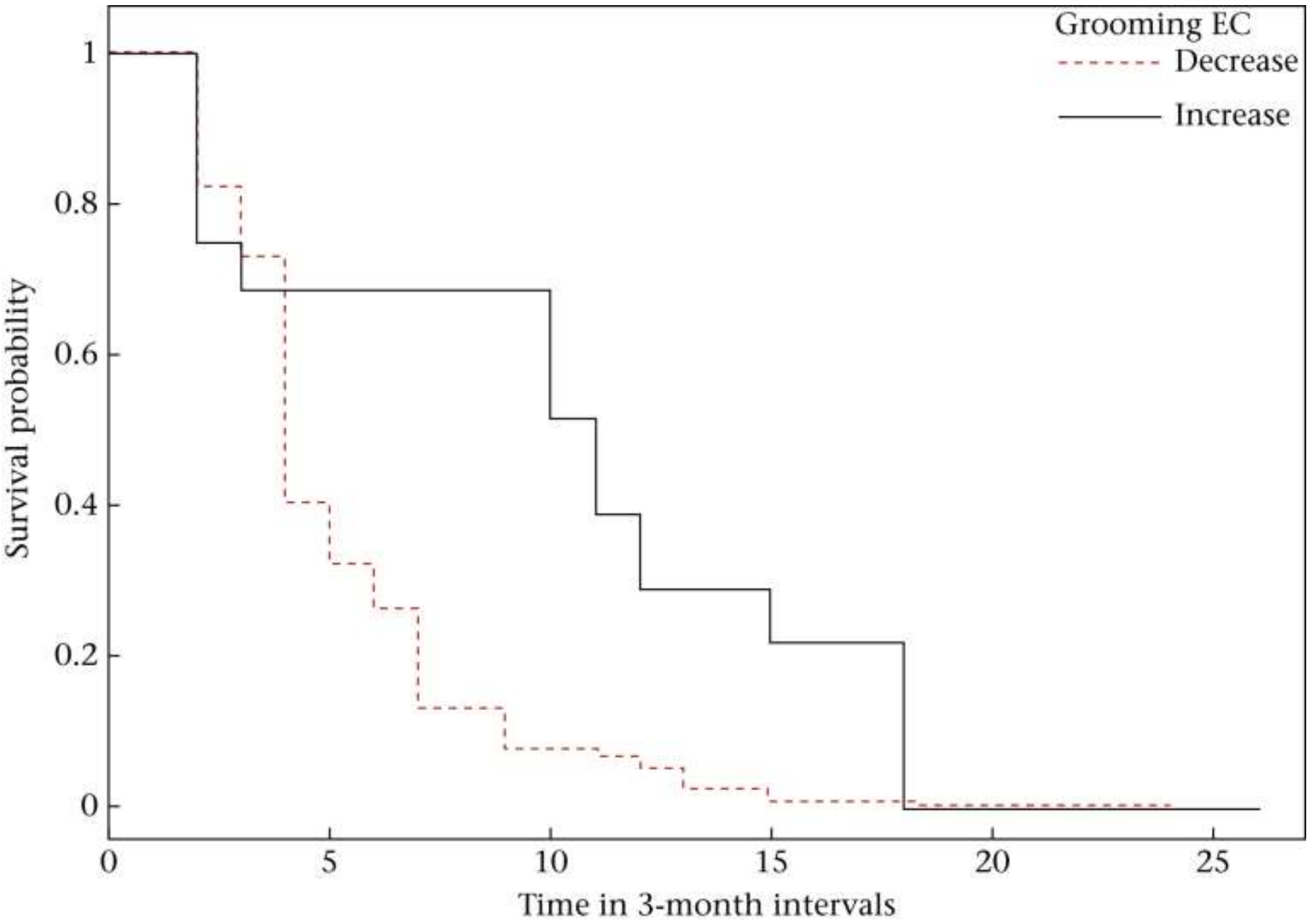

Figure 4. The influence of increasing or decreasing social integration (grooming eigenvector centrality, EC) on the decision to leave a group (model 3). Survival time in 3-month intervals from entry into the group (time 0) is indicated on the *x*-axis.

probability that a male would leave (hazard ratio = 0.59). We found, too, a negative effect of grooming EC difference on the likelihood of emigration. As grooming EC score increased by one unit the probability of emigration dropped by 36% (hazard ratio = 0.64. Table 3, Figure 4). There was little evidence that changes in the other predictor variables influenced a male's probability of emigration.

DISCUSSION

Not unexpectedly, our results confirm that the probability of movement between groups by male vervet monkeys in our study population is seasonally structured, as it is in a subtropical area in South Africa (Henzi and Lucas, 1980). Male dispersal is strongly positively correlated with female reproductive activity (see also Cheney and Seyfarth, 1983), with a peak that precedes the corresponding peaks in mating activity and conception by approximately four weeks. In the absence of an extra-group phase, the close alignment of the rise in dispersal probability with a rise in testicular androgen, although preliminary, suggests that the latter is the proximate physiological trigger that places most males in their new groups in time to take advantage of the rise in conceptive mating opportunities, especially when it may take a month for them to move from the periphery to the centre of the group (Cheney and Seyfarth, 1992). Similarly, dispersal prior to the mating season has been observed in several seasonally breeding primate species (Morelli *et al.*, 2009; Sprague, 1992; Sussman, 1992). While in spotted hyenas (*Crocuta crocuta*) immigrant males have much higher androgen levels than natal males and despite being outranked by all natal males they do gain higher reproductive success in their new group. However, whether increases in androgens trigger dispersal or are a result of males no longer being suppressed by females remains unclear (Holekamp and Smale, 1998).

While immediate access to mating opportunities is undoubtedly important, it is also clear that the real reproductive benefits of residency are tied to tenure length. Unlike chacma baboons (*Papio hamadryas ursinus*), for example, where male rank is fundamentally tied to physical condition and achieved very soon after arrival in to a group (Henzi *et al.*, 2010), vervet males need time to rise in rank. Although initial rank is positively correlated with highest achieved rank, suggesting a role for physical condition, it also takes longer to rise to high rank, indicating the importance of social factors, as does the fact that secondary non-natal migrators rise in rank more rapidly than primary non-natal migrating males, which hints that secondary migrators may be more socially adept. With rank underpinning reproductive success (Minkner *et al.*, 2018), and a median time needed to reach maximum rank of 364 days, it is not surprising that, on average, a male stays in a group long enough to participate in the subsequent mating season (400 days), or that males achieving higher ranks capitalise on this by extending their stay for longer after doing so.

What is more surprising is that a decline in rank is not a factor in a male's decision to curtail his residency, which is presaged instead by a decline in the number of females and his grooming network integration. This is similar to golden lion tamarins (*Leontopithecus rosalia*), where male dispersal is triggered by a reduction in affiliation within their social group (Romano *et al.*, 2019), whereas an unfavourable sex ratio triggers dispersal in howler monkeys (*Alouatta palliata*, Clarke and Glander, 2010), ring tailed lemurs (*Lemur catta*, Sussman, 1992), and brown jays (*Cyanocorax morio*, Williams and Rabenold, 2005). As measures of social and spatial integration are independent predictors of residency length for vervets, it may well be that, in addition to their roles in male rank acquisition (Young *et al.*, 2017a), they also have direct consequences for a male's reproductive opportunities. Vervet females are co-dominant to males, a finding we have argued is tied to their ability to regulate male mating access (Young *et al.*, 2017a). It may be that social integration undercuts or overrides the consequences of rank loss, which is principally likely to be experienced as a declining capacity to prevent other males from mating, and which can be countered by the direct expression of female choice. If so, declining social connectedness would be expected to be a powerful trigger of departure.

The obvious problem with this argument is that our data are correlational: we do not know whether males leave because their network is disintegrating or whether their network centrality declines because an increasing probability of departure makes them disinclined to sustain relationships. As our data indicated, female availability appears to be a powerful enough trigger on its own. To resolve this issue, we need information on the dynamics of male-female interactions over time, so that we can generate a better understanding of who is responsible for the maintenance of relationships over time. We have been collecting relevant data to address this issue and will report on it elsewhere.

Finally, our data allow us to comment on the proposition that vervet male residency is ultimately constrained by the reproductive maturity of putative daughters (Henzi and Lucas, 1980), as observed in other mammalian species where male group residency is relatively long (Jack, 2003); see for example, white faced capuchins (*Cebus capucinus*, Fedigan, 2003), Japanese macaques (*Macaca fuscata*, Sprague *et al.*, 1998), and lions (*Panthera leo,* Pusey and Packer, 1987). While we show that there is strong evidence for a downturn in the probability of residency after 1428 days, this occurs 150 days (~5 months) after the modal age of conception for primiparous females in our population. Consequently, if daughters are setting an upper limit to residency, this is not underpinned by selection for some anticipatory proximate mechanism that results in males emigrating before their daughters are sexually mature, as argued by Henzi and Lucas (1980). Indeed, as shown for capuchins by Muniz *et al.* (2006), there is no need for a male to leave in order to avoid inbreeding, since a proximate mechanism such as phenotype matching (Alberts, 1999), or an aversion to mating with females who were socially associated as non-adults (Westermarck, 1891), will produce the same outcome without incurring the costs of dispersal. Rather, given the importance of female number as a trigger of movement, our results suggest that the sexual maturity of daughters should be seen as exacerbating the perceived decline in available sexual partners.

In conclusion, we provide evidence that females play a role in male secondary dispersal decisions in a seasonally breeding, co-dominant primate society, with male dispersal being triggered by a reduction in social integration as well as absolute female number.

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DECLARATION OF INTESTEST

The authors declare no conflict of interest.

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