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

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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 migration 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, and that 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: Male migration; group residency; tenure length; *Chlorocebus pygerythrus*; social integration; dominance.

INTRODUCTION

Inbreeding avoidance and maximisation of lifetime reproductive success are the two main drivers of dispersal from the natal group and subsequent, secondary migration for males in gregarious mammalian social systems (Greenwood 1980; Pusey & 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 & Lucas 1980; van Noordwijk & van Schaik, 2004).

Where a male's reproductive opportunities are positively tied to his individual dominance rank – which characterises many primate social organisations (Schülke & 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 & 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). The fact that vervet males rise in rank relatively slowly during their tenure (see below) also points to a need to cultivate females to this end 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 no time spent as a solitary animal (Henzi & Lucas 1980). After confirming that male migration maps onto the mating season at our site - 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 this, 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 & Lucas 1980).

METHODS

Study site and subjects

At the Samara Private Game Reserve, South Africa (32°22'S, 24°52'E), we collected data between September 2009 and December 2016 on three groups (PT, RBM, RST) of wild, fully habituated and individually recognisable vervet monkeys, occupying semi-arid riverine woodland (Pasternak et al. 2013). Group composition varied across the three groups and the study period ($N_{\text{RBM Males}}$: 4-19, $N_{\text{RBM Females}}$: 7-17; $N_{\text{RST Males}}$: 5-19, $N_{\text{RST Females}}$: 11-22; $N_{\text{PT Males}}$: 3-12, $N_{\text{PT Females}}$: 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

We used scan sampling (Altmann 1974) at 30-minute intervals to record the general activity (resting, moving, foraging or allo-grooming) of each adult group member and the identities of all its neighbours within a 2 m radius, across each study day (N = 493,756 scans) (McFarland et al. 2015; Pasternak et al. 2013). Each scanning period lasted a maximum of 10 minutes in order to ensure as many animals as possible were sampled (i.e., to permit researchers to identify animals beyond the researchers' immediate vicinity), and most individuals were recorded in each scan. Additionally, for records of allo-grooming, we recorded both the identity of the partner and the direction of grooming. Agonistic behaviours were recorded *ad libitum.*

Dominance rankings and power trajectories

Our study was divided into 3-month blocks fixed by the mating (April-June) and birth seasons (October-December), separated by the January-March and July-September periods. Data from on-going, *ad libitum* observations of decided dyadic agonism (N = 5,212) were then used to construct male-male dominance hierarchies for all adult males in each three-month period. For each group, in each time period, dominance rank was expressed as a standardized normalized David's score (SDS), using the excel macro from the package "DomiCalc" (Schmid & de Vries 2013). We standardized our dominance ranks in order to permit comparisons across groups and time. To do so, we divided each individual's Normalised David's score by the highest score for that period/group, such that the highest ranked individual had a score of one (Henzi et al. 2013). Using decided dyadic agonism, we determined the level of aggression each male received from females over each 3-month block. As our study site is situated in open, semi-arid riverine woodland with high levels of visibility of all group members, we are confident we missed very few agonistic interactions within our groups. We also controlled for observer effort (number of observers per group per scan day; range 1-3) and for the presence of each individual animal in the group on each scan day (based on daily group census of an individual animal's presence/absence within the group).

We estimated each male's power trajectory by determining Elo-ratings (Albers & 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. (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

We described social relationships, using our scan data, to construct spatial (<2 m) and grooming association matrices for each three-month block. In doing so, we controlled for both the number of weeks each male was in each group and for observation effort by dividing each dyadic association score by the total number of scans in which each dyad member was observed. We looked at a male's total level of social integration by examining social relationships between all adult group members. We derived two measures of association from the social network (SN), which have been shown to be important social measures in our population previously (Josephs et al. 2016; McFarland et al. 2015; Young et al. 2017b). We used Eigenvector Centrality (EC), which estimates a male's centrality as a function of his partners' centrality, to estimate the extent of male integration, while degree was used to account for the number of females to which a male was connected and strength to estimate the magnitude of a male's social ties. We considered grooming and proximity association separately, as each targets different network properties (Castles et al. 2014). Our previous research found that, for males, the two most important social measures were grooming EC and proximity degree and thus these measures were included in the present analysis.

Mating and conception

We used observed mating as our index of reproductive access (Freeman et al. 2016; Minkner et al. 2018). We recorded all observed copulations between males and females on our three groups *ad libitum*. Our field site is an open habitat and therefore, given multiple observers, we are confident that we were able to record most copulations without spatial bias. 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.

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 seasonal alteration in androgen production we selected five males, analysing one sample from each over the period Jan – May 2016. 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 extraction as well as enzyme immunoassays (EIA) were conducted at the Endocrine Research Laboratory, University of Pretoria. 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 & 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; median fAM: 623 ng/g DW) and immature (n = 9; median fAM: 209 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 one exception, all statistical analyses were run in R 3.2.2. (R-Core-Team, 2016).

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 & Lund 2011). To describe the relationship between the timing of male migration, mating and conceptions, we used the "forecast" package in R (Hyndman & 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 (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 & Grambsch, 2013), using the "coxme" package (Therneau & 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 & 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 emigrated 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 & Grambsch, 2013). Using the function "vif" from R package "car" (Fox & 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 & Jackson 2008). We used the 'MuMIn' package (Barton & Barton 2015) to generate marginal and conditional R^2 values for the whole models using the function "r.squaredLR" (Nakagawa & 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 & Bolstad 2017) to address the small sample size.

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 migration

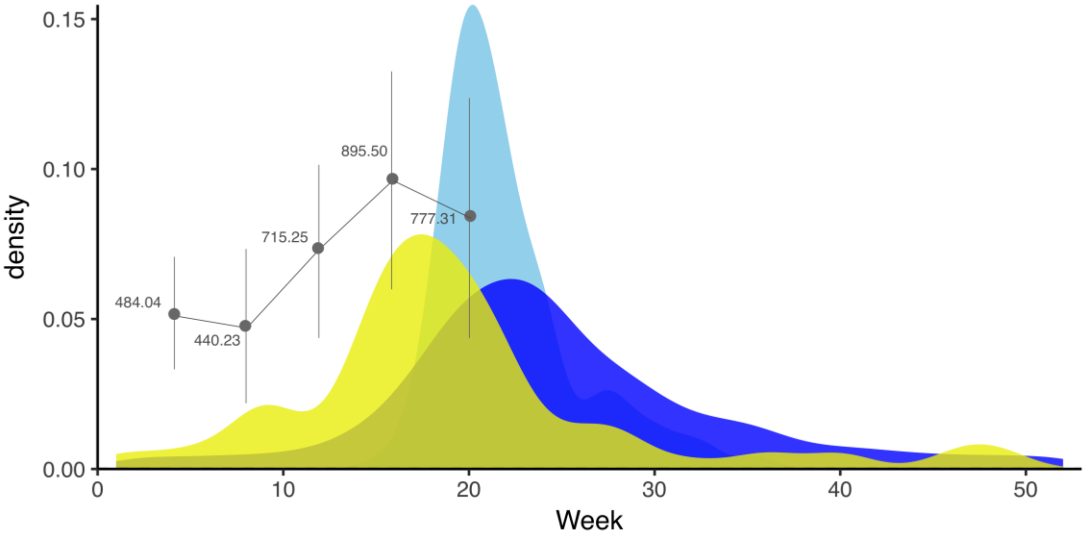
Over the course of the entire study period, 138 males were observed to reside in our study groups. Of these males, 14 are known to have died, 20 males were present at the start of the study (of which 12 had known subsequent emigrations) and 19 males were present at the end of the study period. Of the 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 migrated most frequently in the months of April and May (45 of 63 migrations) and the distribution of migration was not uniform (*Rao spacing statistic* = 297.692, N = 63, P < 0.001). We also found six incidents of parallel migration, where two males from the same group moved on the same day. We had one observation of a 3-year-old juvenile migrating with a 4-year-old and a 5-year-old sub-adult between two of our study groups.

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

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

<Insert figure 1 here>

Figure 1: Showing kernel density estimates of the number of male migration events (yellow), the number of copulations (dark blue) and the number of conceptions (sky blue) per week of the year (1-52 weeks). Also shown are the mean ± SD fAM levels of five males for the months of January to May in order to show the timing of peak androgen production.

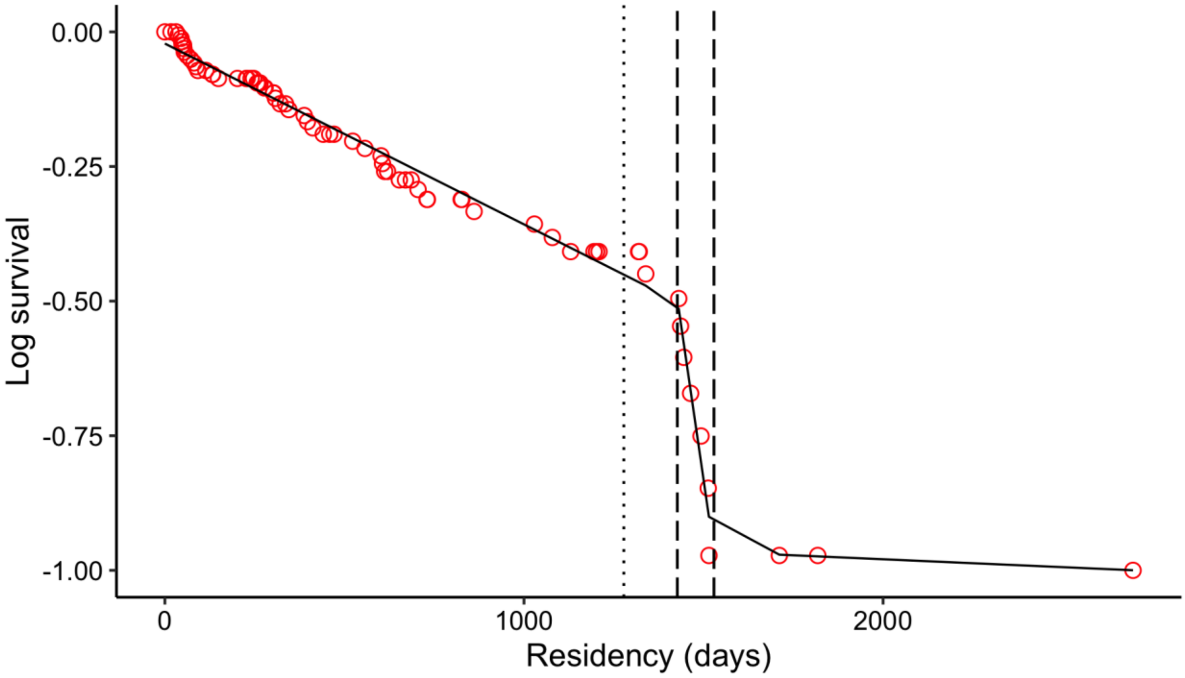


What predicts group residency length?

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 migratory 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 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).

<Insert figure 2 here>

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.



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, $N_{Primary} = 8$, $N_{Secondary} = 9$).

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 whilst grooming EC showed a negative statistical trend (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 a increase in grooming EC of 1 unit decreased the likelihood of departure by 37% (hazard ratio = 0.625).

<Insert table 1 here>

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). Social factors were 1) the highest

rank position a male achieved, 2) the highest grooming EC score a male achieved and 3) the highest proximity degree score a male achieved. N = 44 migratory events plus 32 censored males. 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 migrating.

Factor	**ß ± se**	**Hazard ratio**	**z value**	**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

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).

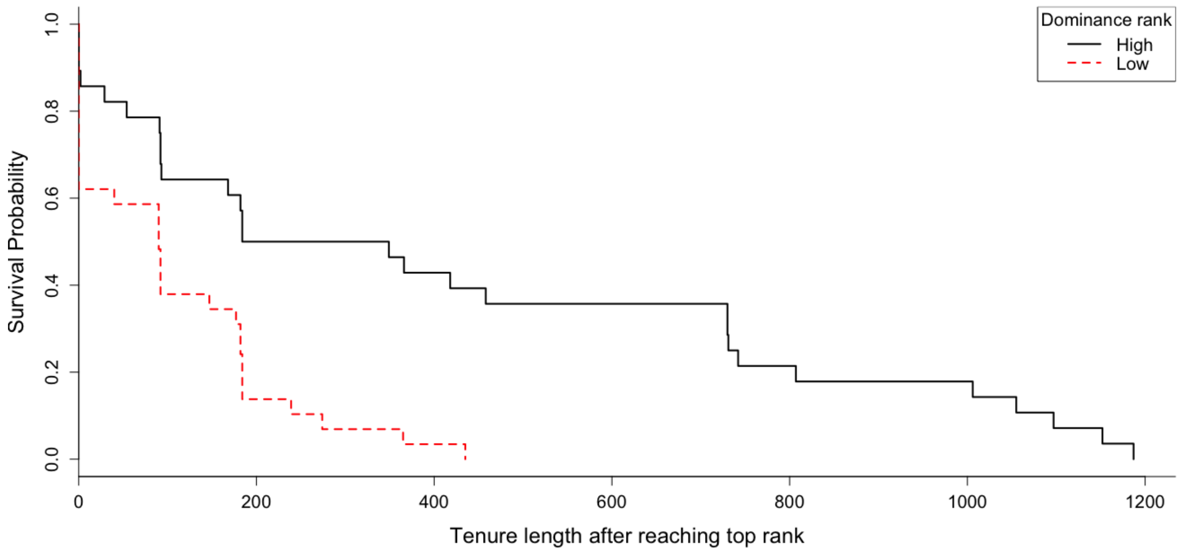
<Insert table 2 here>

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. Social factors were 1) the highest rank position a male achieved, 2) the highest grooming EC score a male achieved, 3) the highest proximity degree score a male achieved and 4) a male's group residency length before achieving their highest rank. N = 44 migratory events plus 19 censored males. 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.

Factor	**ß ± se**	**Hazard ratio**	**z value**	**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

<Insert figure 3 here>

Figure 3: The relationship between rank and male residency length (model 2). The y-axis indicates survival probability, while the x-axis indicates the number of days in residence. For illustrative purposes the data are split into two groups: males of high rank (solid black line) versus males of low rank (dashed red line).



What factors trigger male migratory 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 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.

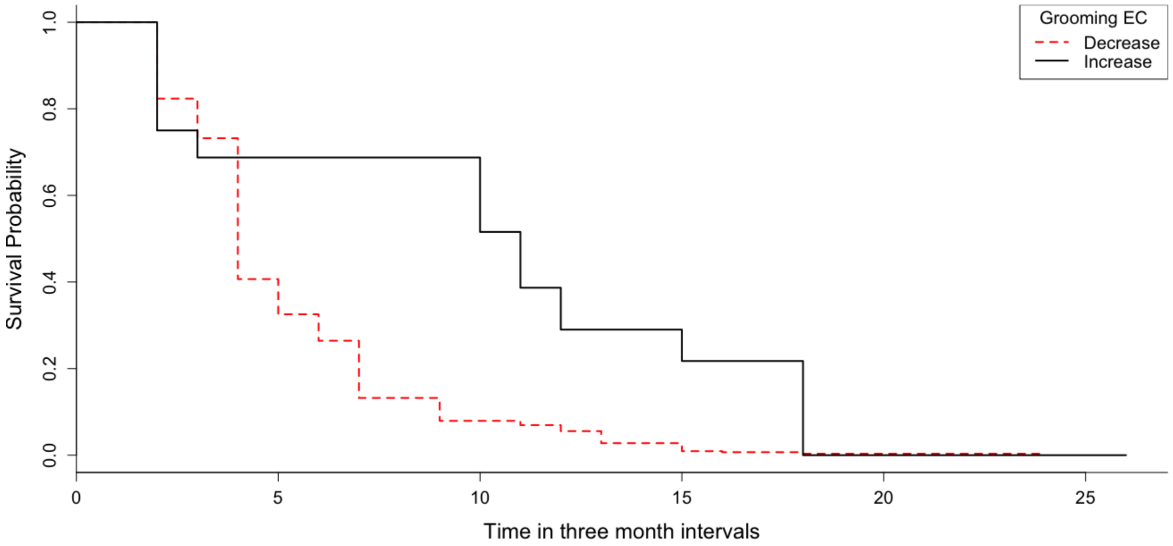
<Insert table 3 here>

Table 3: Output of the cox proportional hazards model to investigate the influence of several social factors on a male's decision to emigrate or not (N = 37 migratory events plus 19 censored males). Social factors were the number of males and females, male standardised rank, male power trajectory, two SN measures (grooming EC and proximity degree), the proportion of female with a dependant infant, and male mating success. 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 migrating.

Factor	**β ± se**	**Hazard ratio**	**z value**	**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

<Insert figure 4 here>

Figure 4: The influence of increasing or decreasing social integration (grooming EC) on the decision to leave a group (model 3). The y-axis indicates the probability of survival, while the survival time in three-month time blocks from entry into the group (time 0) is indicated on the x-axis. For illustrative purposes the data are split into two groups: increase in grooming EC (solid black line) and decrease in grooming EC (dashed red line).



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 & Lucas 1980). Male migratory movement is strongly positively correlated with female reproductive activity (see also Cheney & 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 migration with a rise in testicular androgen, 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 & Seyfarth, 1992).

While immediate access to mating opportunities is undoubtedly important, it is also clear that the real 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, 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. As measures of social and spatial integration are independent predictors of residency length, 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 & Lucas 1980). 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 & Lucas (1980). Indeed, as shown for capuchins (*Cebus capucinus*) 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 migration. 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.

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DECLARATION OF INTESTEST

The authors declare no conflict of interest.

Tables and figures

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). Social factors were 1) the highest rank position a male achieved, 2) the highest grooming EC score a male achieved and 3) the highest proximity degree score a male achieved. N = 44 migratory events plus 32 censored males. 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 migrating.

Factor	**ß ± se**	**Hazard ratio**	**z value**	**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

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. Social factors were 1) the highest rank position a male achieved, 2) the highest grooming EC score a male achieved, 3) the highest proximity degree score a male achieved and 4) a male's group residency length before achieving their highest rank. N = 44 migratory events plus 19 censored males. 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.

Factor	**ß ± se**	**Hazard ratio**	**z value**	**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

Table 3: Output of the cox proportional hazards model to investigate the influence of several social factors on a male's decision to emigrate or not (N = 37 migratory events plus 19 censored males). Social factors were the number of males and females, male standardised rank, male power trajectory, two SN measures (grooming EC and proximity degree), the proportion of female with a dependant infant, and male mating success. 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 migrating.

Factor	**β ± se**	**Hazard ratio**	**z value**	**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
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Figure 1: Showing kernel density estimates of the number of male migration events (yellow), the number of copulations (dark blue) and the number of conceptions (sky blue) per week of the year (1-52 weeks). Also shown are the mean ± SD fAM levels of five males for the months of January to May in order to show 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 3: The relationship between rank and male residency length (model 2). The y-axis indicates survival probability, while the x-axis indicates the number of days in residence. For illustrative purposes the data are split into two groups: males of high rank (solid black line) versus males of low rank (dashed red line).

Figure 4: The influence of increasing or decreasing social integration (grooming EC) on the decision to leave a group (model 3). The y-axis indicates the probability of survival, while the survival time in three-month time blocks from entry into the group (time 0) is indicated on the x-axis. For illustrative purposes the data are split into two groups: increase in grooming EC (solid black line) and decrease in grooming EC (dashed red line).

REFERENCES

Agostinelli, C., & Lund, U. (2011). circular: Circular statistics. *URL http://cran. r-project. org/src/contrib/Descriptions/CircStats. html*,

Albers, P. C. H., & de Vries, H. (2001). Elo-rating as a tool in the sequential estimation of dominance strengths. *Animal Behaviour*, *61*, 489-495.

Alberts, S. C. (1999). Paternal kin discrimination in wild baboons. *Proceedings of the Royal Society of London B: Biological Sciences*, *266*, 1501-1506.

Altmann, J. (1974). Observational sampling of behavior: sampling methods. *Behaviour*, *49*, 227-266.

Barton, K., & Barton, M. K. (2015). Package 'MuMIn'. *ftp://155.232.191.229/cran/web/packages/MuMIn/,*

Bercovitch, F. B. (1988). Coalitions, cooperation and reproductive tactics among adult male baboons. *Animal Behaviour*, *36*, 1198-1209.

Bramblett, C. A., Pejaver, L. D., & Drickman, D. J. (1975). Reproduction in captive vervet and Sykes' monkeys. *Journal of Mammalogy*, *56*, 940-946.

Castles, M., Heinsohn, R., Marshall, H. H., Lee, A. E. G., Cowlishaw, G., & Carter, A. J. (2014). Social networks created with different techniques are not comparable. *Animal Behaviour*, *96*, 59-67.

Cheney, D. L., & Seyfarth, R. M. (1983). Nonrandom dispersal in free-ranging vervet monkeys: social and genetic consequences. *The American Naturalist*, *122*, 392-412.

Cheney, D. L., & Seyfarth, R. M. (1992). *How Monkeys See the World: Inside the Mind Of Another Species*. Chicago, Ill.: University of Chicago Press.

Clarke, P. M. R., Henzi, S. P., Barrett, L., & Rendall, D. (2008). On the road again: competitive effects and condition-dependent dispersal in male baboons. *Animal Behaviour*, *76*, 55-63.

Colquhoun, D. (2014). An investigation of the false discovery rate and the misinterpretation of p-values. *Royal Society Open Science*, *1*, 140216.

Curran, J., & Bolstad, W. (2017). Bolstad: Bolstad functions. *R Package Version 0.2-34. https://cran.r-project.org/web/packages/Bolstad/index.html*,

Dubuc, C., Muniz, L., Heistermann, M., Engelhardt, A., & Widdig, A. (2011). Testing the priority-of-access model in a seasonally breeding primate species. *Behavioral Ecology and Sociobiology*, *65*, 1615-1627.

Fox, J., & Weisberg, S. (2011). *An R Companion to Applied Regression* (Second ed.). Thousand Oaks CA: Sage. Retrieved from http://socserv.socsci.mcmaster.ca/jfox/Books/Companion

Freeman, N. J., Young, C., Barrett, L., & Henzi, S. P. (2016). Coalition formation by male vervet monkeys (*Chlorocebus pygerythrus*) in South Africa. *Ethology*, *122*, 45-52.

Ganswindt, A., Heistermann, M., Borragan, S., & Hodges, J. K. (2002). Assessment of testicular endocrine function in captive African elephants by measurement of urinary and fecal androgens. *Zoo Biology*, *21*, 27-36.

Greenwood, P. J. (1980). Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour*, *28*, 1140-1162.

Henzi, S. P., Clarke, P. M. R., van Schaik, C. P., Pradhan, G. R., & Barrett, L. (2010). Infanticide and reproductive restraint in a polygynous social mammal. *Proceedings of the National Academy of Sciences*, *107*, 2130-2135.

Henzi, S. P., Forshaw, N., Boner, R., Barrett, L., & Lusseau, D. (2013). Scalar social dynamics in female vervet monkey cohorts. *Philosophical Transactions of the Royal Society B*, *368*, 20120351.

Henzi, S. P., & Lucas, J. W. (1980). Observations on the inter-troop movement of adult vervet monkeys (*Cercopithecus aethiops*). *Folia Primatologica*, *33*, 220-235.

Hyndman, R. J., & Khandakar, Y. (2008). Automatic time series forecasting: the forecast package for R. *Journal of Statistical Software*, *26*, 1-22.

JMP, Version 13 (2013). SAS Institute Inc., Cary, NC.

Josephs, N., Bonnell, T., Dostie, M., Barrett, L., & Henzi, S. P. (2016). Working the crowd: sociable vervets benefit by reducing exposure to risk. *Behavioral Ecology*, *27*, 988-994.

McFarland, R., Fuller, A., Hetem, R. S., Mitchell, D., Maloney, S. K., Henzi, S. P., & Barrett, L. (2015). Social integration confers thermal benefits in a gregarious primate. *Journal of Animal Ecology*, *84*, 871-878.

Mills, M. (2011). *Introducing survival and event history analysis*. London: Sage.

Minkner, M. M. I., Young, C., Amici, F., McFarland, R., Barrett, L., Grobler, J. P., Henzi, S. P., & Widdig, A. (2018). Assessment of male reproductive skew via highly polymorphic STR markers in wild vervet monkeys, *Chlorocebus pygerythrus*. *Journal of Heredity*, *109*, 780-790.

Muniz, L., Perry, S., Manson, J. H., Gilkenson, H., Gros-Louis, J., & Vigilant, L. (2006). Father--daughter inbreeding avoidance in a wild primate population. *Current Biology*, *16*, R156-R157.

Nakagawa, S., & Schielzeth, H. (2012). A general and simple method for obtaining Rcol2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, *4*, 133-142.

Neumann, C., Duboscq, J., Dubuc, C., Ginting, A., Irwan, A. M., Agil, M., Widdig, A., & Engelhardt, A. (2011). Assessing dominance hierarchies: validation and advantages of progressive evaluation with Elo-rating. *Animal Behaviour*, *82*, 911-921.

Noë, R., & Sluijter, A. A. (1995). Which adult male savanna baboons form coalitions? *International Journal of Primatology*, *16*, 77-105.

Palme, R., & Möstl, E. (1993). Biotin-streptavidin enzyme immunoassay for the determination of oestrogens and androgens in boar faeces. In S. Görög (Ed.), *Advances of steroid analysis '93* (pp. 111-117). Budapest: Akademiai Kiado.

Pan, Y., & Jackson, R. T. (2008). Ethnic difference in the relationship between acute inflammation and serum ferritin in US adult males. *Epidemiology and Infection*, *136*, 421-431.

Pasternak, G. M., Brown, L. R., Kienzle, S., Fuller, A., Barrett, L., & Henzi, S. P. (2013). Population ecology of vervet monkeys in a high latitude, semi-arid riparian woodland. *Koedoe*, *55*, Art. #1078.

Pusey, A. E., & Packer, C. (1987). The evolution of sex-biased dispersal in lions. *Behaviour*, *101*, 275-310.

R-Core-Team. (2016). *R: A language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing.

Schmid, V. S., & de Vries, H. (2013). Finding a dominance order most consistent with a linear hierarchy: an improved algorithm for the I&SI method. *Animal Behaviour*, *86*, 1097-1105.

Schülke, O., & Ostner, J. (2012). Ecological and social influences on sociality. In J. C. Mitani, J. Call, P. M. Kappeler, R. A. Palombit, & J. B. Silk(pp. 195-219). Chicago: University of Chicago Press.

Therneau, T. M., & Grambsch, P. M. (2013). *Modeling survival data: extending the Cox model*. Berlin: Springer.

Therneau, T. M., & Therneau, M. T. M. (2015). coxme: Mixed effects Cox models. Version 2. *UR L http://CRAN. R-project. org/package= coxme. R package version*,

Therneau, T. M. (2014). A Package for Survival Analysis in S. 2014. R package version 2.37-7. *http://CRAN.R-project.org package=survival*,

van Noordwijk, M. A., & van Schaik, C. P. (2004). Sexual selection and the careers of primate males: paternity concentration, dominance-acquisition tactics and transfer decisions. In P. M. Kappeler & C. P. van Schaik (Eds.), *Sexual Selection in Primates: New and Comparative Perspectives* (pp. 208-229). Cambridge: Cambridge University Press.

Vito, M. R. M. (2008). segmented: An R Package to Fit Regression Models with Broken-Line Relationships. *R News*, *8*, 20-25.

Westermarck, E. (1891). *Human Marriage in The History of Mankind*. London: MacMillan.

Young, C., Hähndel, S., Majolo, B., Schülke, O., & Ostner, J. (2013). Male coalitions and female behaviour affect male mating success independent of dominance rank and female receptive synchrony in wild Barbary macaques. *Behavioral Ecology and Sociobiology*, *67*, 1665-1677.

Young, C., McFarland, R., Barrett, L., & Henzi, S. P. (2017a). Formidable females and the power trajectories of socially integrated male vervet monkeys. *Animal Behaviour*, *125*, 61-67.

Young, C., Ganswindt, A., McFarland, R., de Villiers, C., van Heerden, J., Ganswindt, S., Barrett, L., & Henzi, S. P. (2017b). Faecal glucocorticoid metabolite monitoring as a measure of physiological stress in captive and wild vervet monkeys. *General and Comparative Endocrinology*, *253*, 53-59.

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

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Highlights

- Eight years of male vervet monkey social data across three groups
- Migration is seasonal, peaking with androgen levels but before peak conception
- Residency length positively associated to dominance rank and social measures
- Probability to emigrate negatively associated to female number/grooming effort
- Emigration linked to male rank and mediated by female network integration

Figure 1

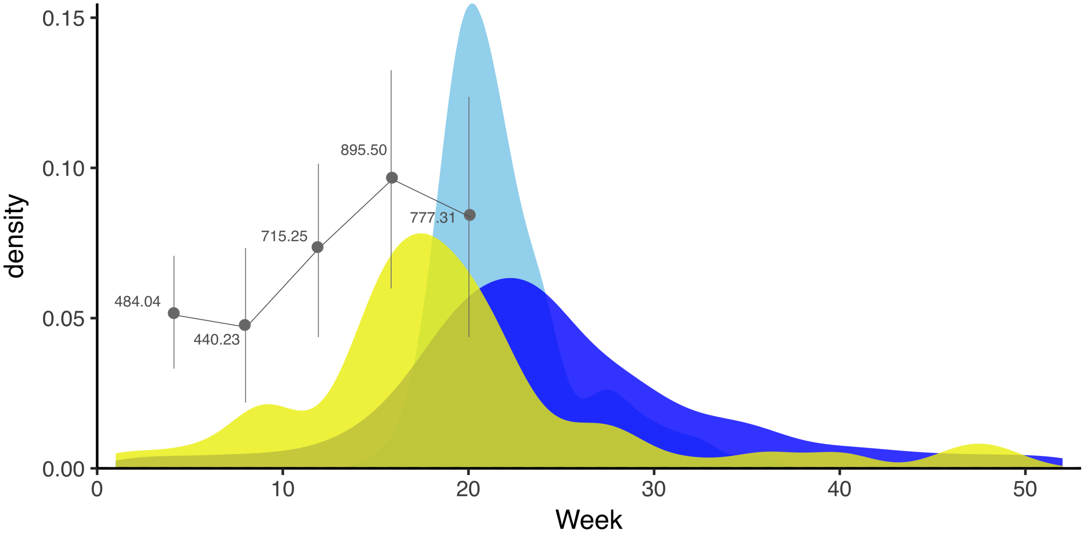
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Figure 2

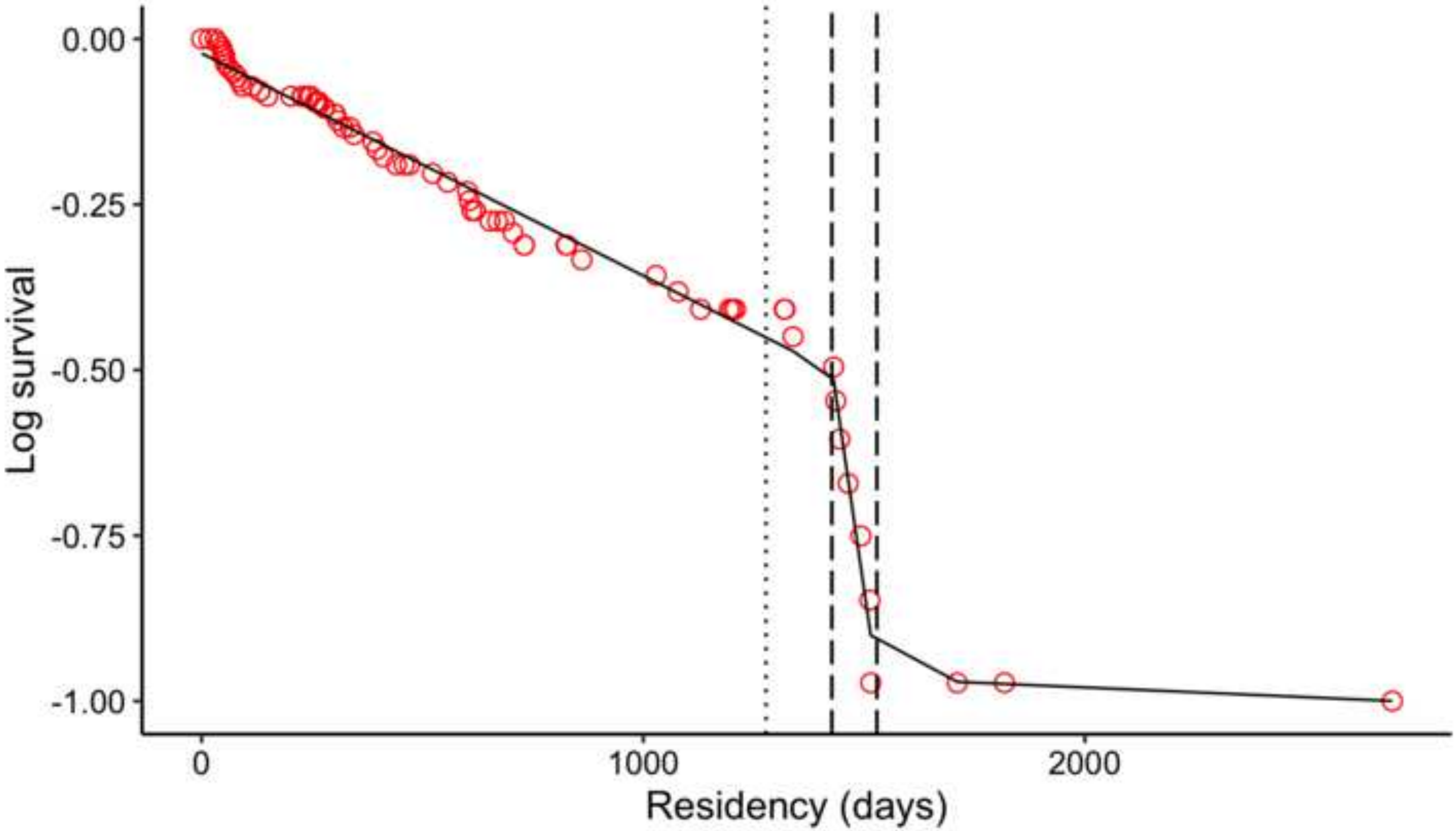

Figure 3

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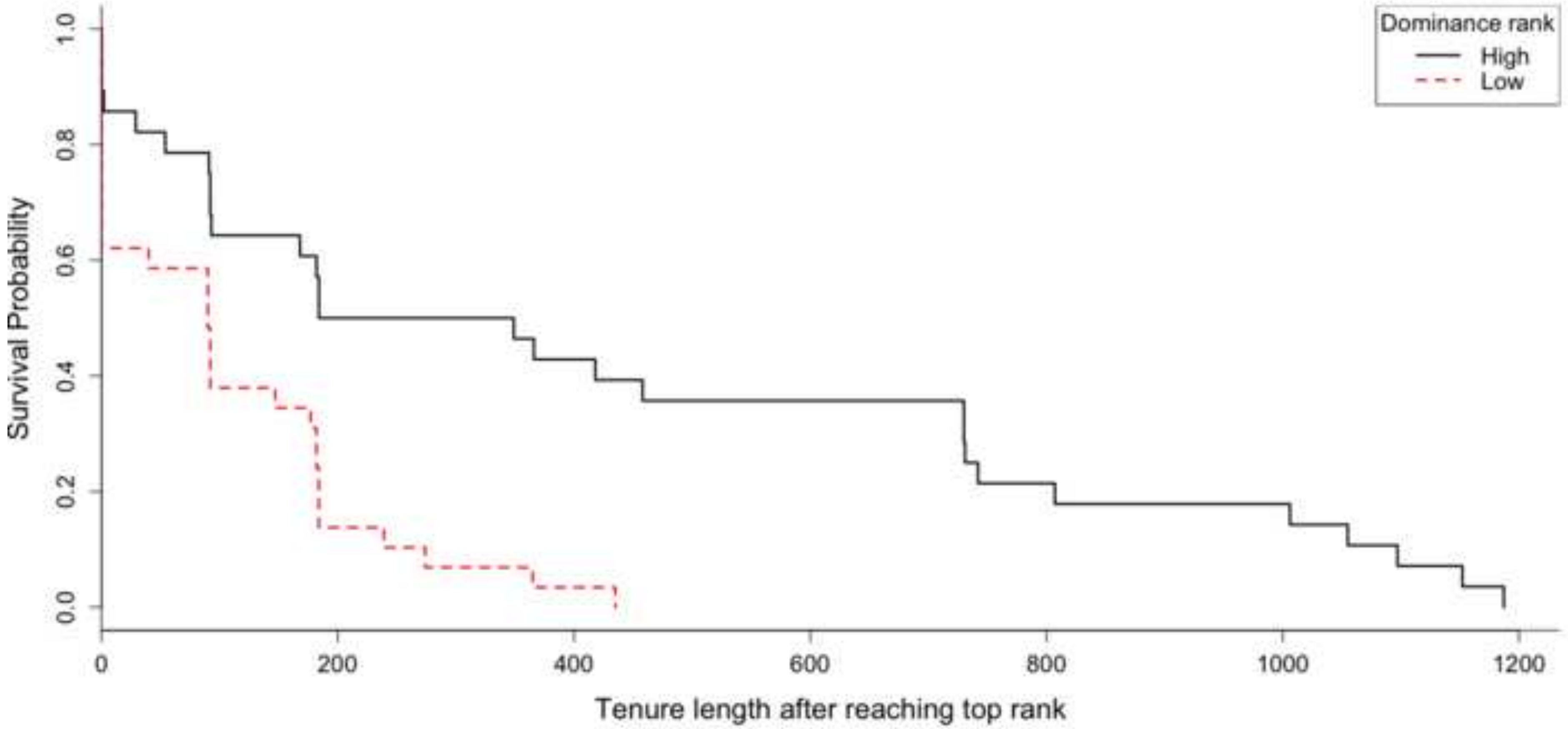
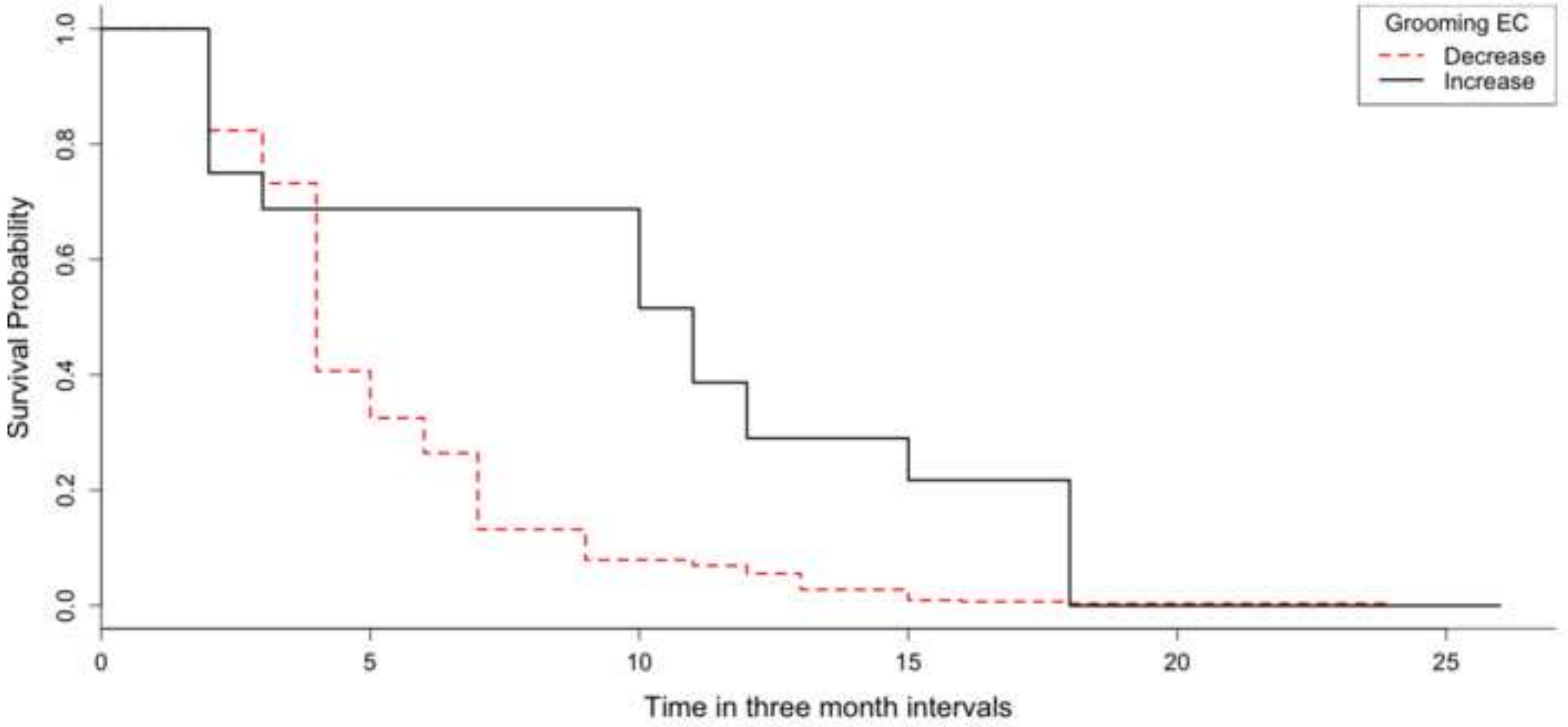


Figure 4


Grooming EC
Decrease
Increase
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0
5
10
15
20
25
Time in three month intervals

*Animal welfare note

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

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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.