The Report Committee for Kara Grace Leimberger
Certifies that this is the approved version of the following report:

Male strategies for changing group membership in Verreaux's sifaka

APPROVED BY

SUPERVISING COMMITTEE:

Supervisor:

Rebecca Lewis

Anthony Di Fiore

Male strategies for changing group membership in Verreaux's sifaka

by

Kara Grace Leimberger, B.S.

Report

Presented to the Faculty of the Graduate School of

The University of Texas at Austin

in Partial Fulfillment

of the Requirements

for the Degree of

Master of Arts

The University of Texas at Austin
May 2015

Acknowledgements

Abstract

Male strategies for changing group membership in Verreaux's sifaka

Kara Grace Leimberger, M.A.

The University of Texas at Austin, 2015

Supervisor: Rebecca Lewis

Males of many group-living mammals disperse to avoid inbreeding and improve their mating opportunities. Different strategies may exist for immigrants, such as replacing the alpha male or entering a group as a subordinate. Verreaux's sifaka (*Propithecus verreauxi*) are highly seasonally breeding lemurs characterized by male-biased dispersal and high within-group reproductive skew. We hypothesized that (1) males time transfers to pursue immediate mating opportunities (i.e., that they enter groups in the pre-mating and mating seasons), (2) males prefer groups with greater reproductive opportunities (i.e., with greater numbers of females), (3) entrances with partners more often result in alpha male replacement, (4) male competitive ability affects immigration strategy, and (5) male competitive ability affects alpha male tenure length. To assess male dispersal strategies, we examined seven years of demographic, morphological, and behavioral data for five social groups of Verreaux's sifaka in the Kirindy Mitea National Park in western Madagascar. Contrary to expectations, we detected no seasonal pattern in immigrations. Males did generally join groups with favorable sex ratios and, to a lesser extent, high numbers of sexually mature females. Transfers occurred individually and in pairs, and a

trend existed for partner presence to increase the likelihood of replacing an alpha male. Pronounced activity of the sternal scent gland (a proxy for testosterone) – but not body mass, canine size, or potential correlates of leaping ability – significantly influenced immigration strategy. Our results suggest that male immigration strategies are affected by group composition and prior dominance status but not reproductive season or morphological indicators of competitive ability. Competitive ability may instead rely on a combination of morphological and behavioral attributes, such as personality, social skillfulness, or coalitionary support. Additionally, fluid group boundaries may allow mating success without establishment in a social group before the mating season.

Table of Contents

List of Tables

List of Figures

INTRODUCTION

Dispersal becomes evolutionarily favorable when benefits accrued outweigh associated costs [Gandon & Michalakis, 2001]. Costs can arise during exploration, transience between permanent groups or sites, and establishment in the new location [Clobert et al., 2009]. Departure into unfamiliar space presents an increased risk of mortality due to predation [Isbell et al., 1990, 1993], increased difficulty navigating and foraging in a novel physical environment [Isbell & Van Vuren, 1996], and potential for sacrificed reproductive opportunities while isolated from potential mates [Alberts & Altmann, 1995]. Additionally, individuals can experience escalated social conflict while establishing status in a new group [Pusey & Packer, 1987; Isbell & Van Vuren, 1996; Bonte et al., 2012] and valuable alliances from the group of origin can be severed [Isbell & Van Vuren, 1996].

Despite these risks, dispersal by one or both sexes occurs commonly among mammals [Greenwood, 1980; Smale et al., 1997] and encompasses both the permanent relocation of pre-reproductive individuals away from the location or group of birth (natal dispersal), as well as subsequent transfer between breeding sites or groups (secondary or breeding dispersal) [Greenwood & Harvey, 1982; Danchin et al., 2001]. Primates generally follow the mammalian pattern of male-biased emigration and female philopatry [Pusey & Packer, 1987; but see Strier, 1994], and lifelong movement between groups is common [e.g., red colobus monkeys: Marsh, 1979; long-tailed macaques: van Noordwijk & van Schaik, 1985; ring-tailed lemurs: Sussman, 1992; Verreaux's sifaka: Richard et al., 1993; squirrel monkeys: Mitchell, 1994; Japanese macaques: Sprague et al., 1998],

1

suggesting that both natal and secondary dispersers accrue benefits, such as inbreeding avoidance [Bengtsson, 1978; Pusey, 1987; Wolff et al., 1988; Clutton-Brock, 1989], avoidance of intrasexual mate competition [Hamilton, 1967; Dobson, 1982; Moore & Ali, 1984], and improved access to mates [Pusey & Packer, 1987].

Individuals may adopt strategies to counter dispersal costs and increase the likelihood of reproductive success [Cheney & Seyfarth, 1983; van Noordwijk & van Schaik, 2001]. Variation in competitive ability may shape dispersal strategies. For example, males with high competitive ability may be more likely to acquire the dominant position in a group by ousting resident males during aggressive takeover events, whereas less competitive males are expected to adopt a low-risk strategy. Poor competitors may enter new groups unobtrusively as subordinates [van Noordwijk & van Schaik, 2001] or may be unable to enter groups at all, instead residing by themselves or in all-male bands [e.g., Hanuman langurs: Sommer & Rajpurohit, 1989]. For example, in species in which immigration by adults is typically aggressive, subadults may be able to avoid antagonism [long-tailed macaques: van Noordwijk & van Schaik, 2001; white-faced capuchins: Jack & Fedigan, 2004b; ursine colobus: Teichroeb et al., 2011], perhaps because residents consider immature individuals inconsequential sexual rivals and thus do not strongly resist their immigration [Richard et al., 1993]. However, direct evidence linking challenge-based entrance strategies to morphological indicators of variable competitive ability is rare.

Leaving and/or entering a group alongside a partner ["parallel dispersal", *sensu* van Hooff, 2000; e.g., squirrel monkeys: Mitchell et al., 1994; white-faced capuchins:

Jack & Fedigan, 2004a,b; ursine colobus: Teichroeb et al., 2009, 2011] can offset

dispersal costs, especially among individuals with low competitive ability. The company

of another individual may reduce predation risk during transit, decrease the risk of injury

from residents upon arrival [Cheney & Seyfarth, 1983], increase the likelihood of

successfully challenging a dominant individual [howling monkeys: Crockett & Sekulic,

1984, Pope, 1990; white-faced capuchins: Fedigan & Jack, 2004], and/or provide a social

ally upon successful group entrance [Pusey & Packer, 1987]. If partners are related to

each other, immigrating together may also provide inclusive fitness benefits [Schoof et

al., 2009]. Accordingly, young primates in some species often transfer alongside brothers

or peers [vervet monkeys: Cheney & Seyfarth, 1983], although high levels of pair

dispersal can occur across all age classes [white-faced capuchins: Jack & Fedigan,

2004a,b; ursine colobus: Teichroeb et al., 2009, 2011].

One important dispersal decision involves which group to join [Danchin et al.,

2001], because certain groups offer higher absolute or relative female availability,

enhancing a male's access to mates [Pusey & Packer, 1987]. Males increase their

reproductive opportunities following secondary dispersal in a number of primates [rhesus

macaques: Drickamer & Vessey, 1973; olive baboons: Packer, 1979; ring-tailed lemurs:

Jones, 1983; yellow baboons: Alberts & Altmann, 1995; olive colobus: Korstjens &

Schippers, 2003; white-faced capuchins: Jack & Fedigan, 2004b], though not universally

[rhesus macaques: Boelkins & Wilson, 1972; long-tailed macaques: van Noordwijk &

van Schaik, 1985; hanuman langurs: Borries, 2000]. When dominant individuals receive

a disproportionate share of reproduction, superior social status following emigration may

enable increased access to reproduction [Borries, 2000; e.g., vervet monkeys: Cheney & Seyfarth, 1983; yellow baboons: Smith, 1992; white-faced capuchins: Jack & Fedigan, 2004b].

Additionally, some time periods may be more favorable for dispersal than others, especially because primates often live in highly seasonal habitats that exhibit variation in resource availability and canopy cover, potentially exacerbating nutritional stress and/or detection by predators [van Schaik & Brockman, 2005]. Furthermore, dispersal during the mating season may yield increased immediate reproductive opportunities in seasonally breeding species [Borries, 2000]. Indeed, some species exhibit concentrated dispersal and/or immigration before and during the mating season [rhesus macaques: Lindburg, 1969, Boelkins & Wilson, 1972, Drickamer & Vessey, 1982; vervet monkeys: Henzi & Lucas, 1980; Japanese macaques: Sprague, 1992; ring-tailed lemurs: Sussman, 1992; hanuman langurs: Borries, 2000; Milne-Edwards' sifaka: Morelli et al., 2009], with sudden, temporary spikes in resident male membership sometimes referred to as "influxes" [patas monkeys: Harding & Olson, 1986; Hanuman langurs: Borries, 2000; blue monkeys: Cords, 2002]. However, other species that exhibit birth peaks do not subscribe to seasonal patterns of dispersal. For example, in long-tailed macaques, immigrations and departures are associated with changes in alpha male membership and subsequent disruption of the male dominance hierarchy instead of the seasonal conceptive peak [van Noordwijk & van Schaik, 2001].

We aimed to (1) describe patterns of male dispersal in a population of Verreaux's sifaka (*Propithecus verreauxi*) at a new site that differs from previous study locations in

key ways, (2) examine how dispersal alters reproductive opportunities for males, (3) investigate factors that influence the probability of an immigrating male replacing an alpha male, and (4) explore how competitive ability influences alpha male tenure length. We predicted that (a) males immigrate during the pre-mating and mating seasons to increase immediate reproductive opportunities; (b) relative to their previous group, adult males improve their future reproductive opportunities by either achieving the same or higher rank post-transfer, or by transferring into groups with more females and more favorable sex ratios; (c) subadult males improve their future reproductive opportunities by selecting groups with more females and more favorable sex ratios compared to nearby groups; (d) males that immigrate with partners are more successful at replacing alpha males; (e) males displaying morphological evidence of low competitive ability enter groups as subordinates; and (f) alpha males displaying morphological evidence of low competitive ability have shorter tenure lengths.

Verreaux's sifaka are medium-sized, diurnal folivores [Richard, 1974]. Social groups comprise between two and 16 individuals [Sussman et al., 2012] characterized by variable sex ratios [Richard, 1985; Richard et al., 1993; Lewis & van Schaik, 2007] and small overlapping home ranges [Richard, 1985; Lewis, 2005]. Females dominate males [Richard & Nicoll, 1987]. Among males, one adult assumes the dominant position [Kraus et al., 1999; Lewis & van Schaik, 2007] and is identifiable by a greasy, stained patch around his sternal scent gland [Lewis & van Schaik, 2007] that is associated with high testosterone levels [Lewis, 2009]. Females asynchronously enter a brief period of receptivity during an annual mating season [Brockman, 1999; Mass et al., 2009].

5

Although extra-group matings occur [Lawler et al., 2003], dominant males sire the majority of a group's infants [Kappeler & Schäffler, 2008]. Copulations by males aged three and four years have been observed [Richard et al., 2002]; however, they rarely result in offspring [Lawler et al., 2003].

While female dispersal occurs, male dispersal is much more common [Richard et al., 1993; Kubzdela, 1997; Kappeler & Fichtel, 2012]. Males generally disperse from their natal group between three and six years of age [Richard et al., 1993; Kappeler & Fichtel, 2012]. Secondary transfer occurs frequently [median male tenure = approx. three years: Richard et al., 1993], with some males transferring twice annually [Brockman et al., 2001]. Sifaka may exhibit a seasonal re-shuffling of reproductive opportunities: approximately one third of male transfers occur during the birth season in one population of Verreaux's sifaka [Brockman et al., 2001], and dispersal rate peaks in the months preceding the mating season occur in Milne Edwards' sifaka [Morelli et al., 2009]. Extra-group and peripheral males [Richard et al., 1993; Lewis, 2004; Kappeler et al., 2012; Port et al., 2012] are observed more often during the mating season [Richard, 1974] and sometimes travel and immigrate into groups as pairs [Jolly et al., 1982; Richard et al., 1993; Kappeler et al., 2012]. Transferring males rarely reside more than two home ranges away from their group of origin [Richard et al., 1993; Richard et al., 2002].

Changes in dominant male membership can occur via aggressive takeovers [Brockman et al., 2001; Kappeler et al., 2009], and male immigrations have been linked to infanticide [Brockman et al., 2001; Lewis et al., 2003; Littlefield et al., 2010].

Competition among males for group vacancies can be extremely intense [Port et al., 2012] with extended bouts of chasing associated with immigration attempts [Richard 1992]. Thus, selection for enhanced male competitive ability is expected. Specifically, intermediate body mass and larger lower limbs may contribute to a "stream-lined" body shape well-suited for the arboreal chasing contests of these vertical clingers and leapers [Lawler et al., 2005]. Immigration by young males is often uncontested, perhaps because they do not pose immediate threats to residents' reproductive opportunities [Richard et al., 1993].

The majority of research on Verreaux's sifaka has come from the dry deciduous Kirindy Forest (KF) and the spiny and gallery forests of Beza-Mahafaly Special Reserve (Beza) in western and southwestern Madagascar, respectfully. While these two populations exhibit similarities (e.g., male-biased dispersal and male-biased sex ratios [Richard et al., 2002; Kappeler et al., 2009]), differences exist in population densities and predation levels [Kappeler & Fichtel, 2012], reproductive skew [Mass et al., 2009], and degree of sexual dimorphism [Lewis & Kappeler 2005]. More recently, the Sifaka Research Project was established at the Ankoatsifaka Research Station in the Kirindy Mitea National Park (KMNP), a forest that encompasses the transition between the KF and Beza habitat types and has intermediate rainfall. The KMNP sifaka population is substantially less dense than previously studied populations (approx. 40 individuals/km^2 [Lewis & Rakotondranaivo, 2011], or seven to nine groups/km^2, versus 24-28 groups/km^2 [Kirindy Forest: Kappeler et al., 2012; Beza Mahafaly: Richard et al., 1991]). Perhaps densities differ because (a) no river is in the study area, and/or (b) *Tamarindus indica*, a

dry season food source [Norscia et al., 2006] whose abundance is associated with Verreaux's sifaka population density [Simmen et al., 2012], is absent from the Ankoatsifaka Research Station [Nagy, 2007]. In addition to these ecological differences, demographic differences exist among the sifaka populations, such as even or female-biased group sex ratios at KMNP [Leimberger & Lewis, 2015], unlike the male-biased sex ratios found in the KF and Beza populations [Richard et al., 2002; Kappeler et al., 2009]. Hence, in addition to explicitly examining seasonal patterns of dispersal and the physical attributes associated with male takeovers, our goal was to expand studies of sifaka dispersal to include a newly studied population with important ecological and demographic differences.

METHODS

Subjects and Datasets

Between 2006 and 2013, 68 individuals were captured and collared with distinctive tags, including 38 males in nine social groups. Between January 2007 and June 2014, four habituated groups were censused monthly, a fifth group was censused most months, and the remaining groups were censused opportunistically. Intermittent gaps occur in the dataset, such as after Cyclone Fanele. Data with monthly resolution or less were used in order to infer the circumstances surrounding immigration (i.e., category of alpha male replacement and presence of partners) and to delineate the time interval in which the event occurred, resulting in 261 group-months of census data distributed across the five main study groups (22 total group-years) (Table 1). Our analysis excluded data from a wandering group of two males (one subadult, one adult) and an adult female because the group persisted for a maximum of six months and did not become established. Behavioral data, similar to those recorded by Lewis [2004, 2008], were collected on a rotating schedule such that each group was generally observed for three consecutive days twice per month. The observations increased the temporal resolution of our group membership dataset beyond that of the monthly censuses and allowed us to verify the consistent presence of any unmarked immigrants.

Animals were sedated following Lewis [2009] during captures conducted annually within a 4-week period in June and July. Morphological measurements collected from captured animals included proxies of fighting ability (body mass and canine length) and potential measures of leaping ability (thigh circumference and lower limb length).

9

Left and right upper canine lengths were averaged for each individual. Thigh circumference and lower limb length were divided by the cube root of body mass to account for allometric effects on linear measurements, as well as to control for variation in body mass between individuals [cf. Lawler et al., 2005]. For the analyses presented here, we included morphological measurements from the capture event closest in time to the immigration event and omitted individuals for which more than 12 months elapsed between capture and transfer. Due to the rapid growth of subadults, we omitted morphological data collected from subadults more than six months before their immigration.

All data collection procedures were approved by the University of Texas at Austin Institutional Animal Care and Use Committee (protocol numbers 05101801, 08110301, and AUP-2011-00143) and adhered to the legal requirements of Madagascar and the American Society of Primatologists (ASP) Principles for the Ethical Treatment of Non-Human Primates.

Definitions

A male was considered a group "resident" if he was present in the group for at least one month, whereas an individual for which at least a month of presence could not be confirmed was termed a "visitor" [cf. Richard et al., 1993]. Accordingly, residence was indicated by presence for at least two consecutive monthly censuses (assuming overall continuity of presence between); or, when data of finer resolution were available from behavioral observations, at least 75% of the observation dates in the month

following the first date that the individual was observed in the group. If a male rejoined a group after being absent for at least a month, i.e. for two consecutive monthly censuses, or for at least 75% of the observation dates in the month following the first date we observed his absence, his return was scored as a separate entrance event. Males "immigrated" into a study group if they joined and became residents. A subset of immigrations were designated "transfers", in which the entering male was known to have resided in a study group (or groups) prior to the immigration event. Males immigrated with "partners" when two to three males joined a group in between observation dates a month or less apart.

We used presence or absence of chest staining during censuses and captures, supplemented with behavioral observations of submissive chatter vocalizations, as an indicator of male dominance [cf. Lewis & van Schaik, 2007] and testosterone levels [Lewis, 2009]. A change in stained male was termed an "alpha male replacement". We scored departure of the resident stained male and entrance of a future resident stained male as a "takeover". "Succession" occurred when an "unstained" subordinate resident male assumed the alpha position following emigration or death of the previous alpha male and transitioned to being "stained". We were not able to determine if the departing male did so voluntarily, or if aggression from a resident male may have incited the emigration. A "waltz-in" [cf. Fedigan & Jack, 2004] occurred when a male or males joined a group with no resident stained male, i.e., when a stained male was not present for at least one observation date prior to an observation date with a different stained male. "Entrance as subordinate" applied to cases where an individual entered a group and the

alpha male membership did not change, or if they entered with a partner that replaced the alpha male.

Debate exists among primatologists about whether sifaka reach adulthood at three [Richard et al., 2002; Kappeler et al., 2009] or five [Lawler et al., 2003; Lewis & van Schaik, 2007] years of age. We assigned sifaka to the following age classes: infants (< 1 year), juveniles (1-2 years), subadults (3-4 years), adults ($\geq$ 5 years). For immature individuals not born during the study, we estimated age by subjectively evaluating tooth wear, dental development, and morphological measurements but were unable to assign ages for adults. Because nearly all births occur in July and August [Lewis & Kappeler, 2005], animals were considered to have transitioned into the next year of life on the first day of September each year. We divided the calendar year into four equal seasons: Mating (January-March), Gestation (April-June), Birth (July-Sept), and Pre-mating (October-December).

Analysis

All analyses were conducted using the statistical programming software R, version 3.1.2 (R Core Development Team, 2014) with significance level set to $\alpha < 0.05$. Kaplan-Meier survival analysis [Kaplan & Meier, 1958] was employed to account for right-censored alpha male residence lengths, which arose when the study period ended mid-tenure. Median tenure estimates and 95% lower confidence limits were obtained using the "survival" package and "survfit" function [Therneau, 2014]. Upper confidence limits for median tenure estimates could not be derived from our survival curves. In order

to include all study groups with known alpha males (N=7 groups), continuous residence between census dates was assumed, even during gaps in data collection if the same male was present before and after the gap. Tenure length calculations were based on the interval between the first census date the male was observed in the group and the last census date the male was observed in the group. Hence, reported median tenure length is an underestimate. One unnatural death was scored as right-censored. Multiple tenure lengths (N = 2) existed for one male but were included because the tenure lengths were considered different enough (93 versus 1614 days) not to bias the tenure estimate in one direction or the other [cf. Alberts & Altmann, 1995]. Left-truncated tenures (N=6) were included because omitting them did not alter the median tenure length estimate.

Sample size limitations precluded the use of survival analysis techniques to examine how competitive ability influences tenure length, so we explored this prediction by running separate analyses for tenure lengths (a) including right-censored observations and (b) excluding right-censored observations. Scatterplots and Spearman's rank correlations were used to visually and statistically examine any patterns present. Additionally, we compared mean values of morphological measurements of individuals employing different immigration strategies (i.e., entering as subordinate versus not entering as subordinate) using parametric and non-parametric t-tests.

In order to detect seasonal patterns in entrances, we used generalized linear mixed models (GLMMs) to account for the pseudoreplication introduced by multiple observations per individual [Hurlbert, 1984; Machlis et al., 1985]. The timing of immigration was scored as the month in which the animal arrived in the destination

13

group. A mixed effects logistic regression model was created using the binary response variable "Did the subject arrive (1/0)?" for each of the four seasons, the fixed effect of "season", and the random effect of "subject". The model was implemented with the "glmer" function contained in the "lme4" package [Bates et al., 2014] with binomial error structure (logit link). The model with all effects was compared to the null model (random effects only) using a likelihood-ratio test. Odds ratios were calculated by exponentiating the GLMM coefficient estimates.

The reproductive opportunities afforded by target group choice were evaluated using two demographic proxies of reproductive competition: sex ratio and number of females. Sex ratio calculations did not include subadult males because they pose inconsequential reproductive competition to adult males [Lawler, 2003]. We calculated sex ratio and female number with and without subadult females, which may represent the future opportunities associated with a group. Improvement of reproductive opportunities was assessed differently for subadult and adult sifaka. For subadults, which were more likely to have been natal to their original group, the group joined was compared to all the other focal groups around the time of transfer. For adults, we only compared the pre-transfer and post-transfer groups. Data for each group were selected from the census date prior to the first date the focal individual was listed in their destination group. Focal individuals were not included in any group composition measures. For subadults, the total number of immigrations included in the comparisons varies per group composition measure, because comparisons were not made between groups when no group variation existed.

14

RESULTS

Total group size over all groups and census dates ranged from 2 to 11 individuals (mean=6.2 ± 1.2 SD individuals, median=6.3) with 1 to 3 adult females (mean=1.7 ± 0.4 SD individuals, median=2.0) and 0 to 3 adult males (mean=1.3 ± 0.2 SD individuals, median=1.0) (Table 1). All groups except one had multiple resident adult males at some point during the study period (Fig. 1). Median tenure length of alpha males (N=18 tenures) was 1317 days (3.6 years), with a lower 95% confidence limit of 568 days (1.6 years) (Fig. 2). Known natal males dispersed from focal groups between 3.1 and 5.4 years of age (mean=4.2 ± 0.9 SD years, median=4.4, N=5).

Fifteen males immigrated into focal groups. Because three males immigrated twice each, 18 total immigrations occurred. Due to the simultaneous entrance of multiple individuals into a group, these immigrations were divided into 15 "immigration events" for a rate of 0.7 immigration events per group-year, or 0.1 immigration events/group/year. In 40% of immigration events (N = 6), alpha male membership changed. Eight out of nine subordinate entrances (89%) were by subadults, who always entered groups as subordinates. Context was determined for seven occurrences of alpha male replacement: two (29%) were waltz-ins, four (57%) were takeovers, and one (14%) transpired via succession. Out of ten immigration events occurring during periods of census data collection with at least monthly resolution, four events (40%) involved partners. Partner immigrations involved two (N=3 events) or three individuals (N=1 event). All immigrations involving partners were associated with alpha male replacement, while most solitary immigrations were associated with no change in the alpha male

15

(Fisher's exact test: P=0.08). Two out of five immigrations by subadults (40%) involved partners, compared to five out of nine immigrations by adults (56%). Adults and subadults immigrated together.

Season did not significantly predict male immigrations (Table 2, χ^2=6.46, df=3, P=0.091). Nevertheless, the odds of successful entrance into a group were lowest during the birth season, two times higher in the mating season, six times higher in the gestation season, and 11 times higher in the pre-mating season. No successful entrances by adults were observed in the birth season, though two subadults successfully transferred (Fig. 3).

Few data were available to statistically evaluate how dispersal decisions alter reproductive opportunities, but preliminary results suggest that, especially for subadults, the group chosen offered increased reproductive opportunities compared to nearby groups. Seven subadult males immigrated into focal groups during periods for which group composition data were available for at least three other focal groups, enabling comparisons to be made. In all cases, subadults chose groups with the most favorable sex ratios and numbers of females while avoiding groups with lowest female availability (Table 4). Transferring subadults always joined a group adjacent to their group of origin. Three adult males transferred between focal groups for which group composition was known before and after transfer. Immigrants chose destination groups with more females in 67% of immigrations and with more favorable sex ratios in 100% of immigrations (Table 5). One of the males increased his rank after transfer, one remained dominant, and one remained subordinate. Results do not vary for either male age class when subadult females are included in demographic measures.

16

Neither canine size (Welch's *t*-test*: t*=0.92, df=4.8, P=0.40) nor lower limb length (Student's *t*-test*: t*=-1.68, df=9, P=0.13) nor thigh circumference (Student's *t*-test: *t*=0.86, df=8, P=0.41) were significantly smaller for individuals that entered as subordinates compared to those that entered as dominants (Fig. 4). A nonsignificant trend existed for larger body mass among individuals that entered as dominants (Student's *t*-test: *t*=2.23, df=9, P=0.052) (Fig. 4). With subadults excluded, greater overlap existed between the body masses associated with each entrance strategy (Fig. 4). Despite stabilizing selection for intermediate body mass in Verreaux's [Lawler et al., 2005], body mass measurements did not seem to cluster around intermediate values in our sample of males involved in alpha male replacement (Fig. 4). Alpha male replacement was more likely when entering males had stained chests at the time of transfer, or when males entered with a partner who had a stained chest (Fisher's exact test: P<0.01). No significant effects of morphological measurements on alpha male tenure length were detected (Table 3, Fig. 5).

DISCUSSION

Male dispersal patterns can be shaped by the spatial and temporal distribution of reproductive opportunities, demography, and innate abilities. Importantly, variation in demography and ecology occur across sifaka populations, and thus male dispersal patterns and social relationships may vary as well. Contrary to expectations, immigration was not strongly associated with seasonality or morphological measures of competitive ability. Additionally, we found that alpha male replacement tended occur when males immigrated into a group with a partner and when immigrants displayed chest staining, an indicator of male dominance and testosterone levels. Dispersing males did not necessarily improve their dominance status, but they did improve their reproductive opportunities by entering groups with greater female availability. Because the majority of alpha male replacements involved males from previously unknown groups preventing an analysis of rank changes, this result must be considered preliminary.

Sifaka groups interact frequently [Richard, 1985; Lewis, 2004], and often peacefully [Lewis, 2004], due to their highly overlapping home ranges [Lewis, 2005]. Thus, waltz-ins may have involved competition for the alpha vacancy between informed contenders from neighboring groups rather than fortuitous discovery. Indeed, at KF a resident male vacancy occurred only once in 127 group-years (0.008/group-year) and was filled within 11 days [Port et al., 2012]. By contrast, we noted two waltz-ins during our much shorter study (0.09/group-year), and once following a six-month vacancy, suggesting that vacancy discovery rate may be influenced by population density and home range overlap differences between the two sites. Consistent with previous research at Beza Mahafaly

18

[Richard et al., 1993, 2002], immigration events at KMNP often occurred among adjacent groups. While long periods of vacancy call into question the attentiveness of neighboring males, other factors, such as female influence over group membership [Lewis, 2008] and risk of inbreeding due to short dispersal distances [Richard et al., 1993] may preclude certain males from immigrating.

Contrary to previous studies of sifaka [Verreaux's sifaka: Richard, 1974; Milne-Edwards' sifaka: Morelli et al., 2009], we found only a nonsignificant trend for male seasonal immigration, perhaps because the monthly resolution of our census dataset did not detect short term male movements, such as temporary influxes by roaming or visiting males that often occur during the mating season [Richard, 1974; Brockman, 1999; Lewis, 2004]. In addition, our division of the year into four equal seasons differed from previous studies. The majority of immigration events occurred during the six month combined pre-mating and mating season, similar to the pattern observed in ring-tailed lemurs [Sussman, 1992]. However, our analysis did highlight that the timing of dispersal may be influenced by more than just immediate mating opportunities (Fig. 2). Because our dataset reflected successful entrances but not failed attempts, variation in immigration timing may reflect the outcome of group residents' variable motivation to expel intruders. Unlike at Beza Mahafaly [Brockman et al., 2001], successful immigration of adult males was never seen in the birth season. Interestingly, infanticide occurs at multiple sites in Verreaux's sifaka [KF: Lewis et al., 2003; Beza Mahafaly: Littlefield, 2010], and resident adult males may more actively defend their offspring and group membership during the birth season when infants are young and particularly vulnerable [Brockman et al., 2001].

19

Moreover, within a framework of dynamic group membership [cf. "neighborhoods": Jolly, 1966], a seasonal dispersal pattern may be less expected and group residency may be a less critical mating strategy than neighborhood membership. Indeed, unlike mating patterns in Milne-Edwards' sifaka [Morelli et al., 2009], extragroup copulations are not uncommon [Brockman, 1999; Lawler, 2007; but see Kappeler & Schäffler, 2008]. Furthermore, an alpha male vacancy due to death or voluntary emigration might feasibly incite a cascade of reshuffling within the population, independent of seasonality. For example, social instability incites male dispersal in long-tailed macaques [van Noordwijk & van Schaik, 2001] and female dispersal in ursine colobus [Teichroeb et al., 2009; Sicotte et al., this volume]. Indeed, "chain migrations" have been observed at all Verreaux's sifaka sites [Berenty: Jolly et al., 1982; KF: Kappeler & Fichtel, 2012; Beza: Lewis, pers.obs.; KMNP: this study]. This clustering of immigration and departure events may reflect interconnected movements within a neighborhood.

Adult males were less likely than subadult males to select groups with high female availability, consonant with Richard et al. [1993]. Because males transfer multiple times over their lifespans, older males may eventually exhaust reproductive options within the neighborhood and be forced to transfer successively farther distances [Richard et al., 1993] to avoid mating with their daughters, a pattern observed among other species exhibiting frequent secondary dispersal [vervet monkeys: Cheney & Seyfarth, 1983; long-tailed macaques: van Noordwijk & van Schaik, 2001; Fedigan & Jack, 2004]. In KMNP, subadults comprised 75% of males that transferred between known social groups, whereas adults accounted for 75% of the males that entered from non-focal

groups (and potentially more distant home ranges). Because subadults are clean-chested males who can enter unobtrusively [Lewis & van Schaik, 2007], they potentially have more options, possibly explaining their consistent selection of favorable groups. In addition, as relatively poor competitors, subadults may be more attuned to the number of excess male competitors and use group composition metrics such as sex ratio, rather than absolute female number [Clarke et al., 2008]. However, our preliminary observations suggest that subadults used both relative and absolute measures, while adult males predominately used sex ratio. Further data are needed to explore whether these differences are reflective of a general pattern.

Entrance strategy and tenure length were unrelated to competitive ability, except for chest staining and age class. Immigrating males that exhibited stained chests had a history of dominance in other social groups, suggesting that they may have been more experienced competitors. Moreover, chest staining in sifaka is associated with higher testosterone levels and possibly increased aggression [Lewis, 2009]. Subadult males have clean, unstained chests [Lewis & van Schaik, 2007], smaller body masses than adults [Lawler, 2006], and may not have accumulated much competitive experience. Given this combination of traits, pursuit of a subordinate entrance strategy by subadults is not surprising. We suspect that other morphological measurements of competitive ability lacked explanatory power due to one or more of the following factors. First, partner entrances potentially confound the effect of individual competitive ability on entrance strategy. Sifaka form coalitions to chase away extra-group males [KF: Lewis, 2004], and thus, coalition formation may be an important alternative strategy for expelling a resident

21

alpha male. Although we could not differentiate between simultaneous immigrations and sequential immigrations, entrances with partners may facilitate replacement. In other species, small-sized or low-ranking individuals sometimes use personality [great tits: Verbeek et al., 1996, Cole & Quinn, 2012; cichlids: Riebli et al., 2011; sticklebacks: Ward et al., 2004], social skills [olive baboons: Sapolsky & Ray, 1989], and problem-solving abilities [chimpanzees: Kummer & Goodall, 1985] to develop alternative strategies to gain access to resources monopolized by dominants [Reader & Laland, 2001]. Second, the difference in competitive ability between alpha males and challengers may be more important than absolute competitive ability. Third, our broad category of "adult" may encompass age-related variation in body mass, which can increase steadily until around year eight [Lawler, 2006]. Finally, competitive ability probably transcends individual morphological characteristics. For instance, agility and endurance may be of utmost importance during chases that span several hours in length [Lawler et al., 2005], but these traits are difficult to measure in the wild.

Our dispersal data also speak to the unusual composition of Verreaux's sifaka groups, which often contain multiple adult males despite small overall group size. Based on behavioral observations, Lewis [2004, 2008] suggested that multimale groups occur in Verreaux's sifaka because both females and the dominant male benefit from the presence of subordinate males, noting that resident males form coalitions against extra-group males and that females encourage group membership for subordinate males. By contrast, other studies have used demographic data to explore why dominant males do not exclude additional (subordinate) males and found that groups with more males do not experience

less frequent takeovers [Kappeler et al., 2009; Port et al., 2012] or higher infant survival [Port et al., 2012]. Using a demographic modeling approach, Port et al. [2012] further concluded that lone "floater" males not only offer no benefits to resident males, but also threaten their continued reproduction. Thus, subordinates may only be able to join groups as subordinates because the costs of excluding them is too high [Port et al., 2012]. Port et al.'s [2012] idea implies that dominants reluctantly tolerate subordinates and do not constitute a concerted unit, but our behavioral observations in dispersal contexts suggest otherwise. Pair takeovers, by default, result in a multi-male group composition, at least temporarily. Moreover, in at least two cases at KMNP, pairs of males moved together from one social group to another, implying that at least some incentive existed to preserve co-residence. Incorporating pair immigrations into future models of multimale group formation may be an important consideration for understanding Verreaux's sifaka social organization.

While our results must be considered preliminary due to small sample size, some interesting patterns in male sifaka dispersal strategies emerged. In particular, age and dominance status seem to influence dispersal decisions such as entrance strategy. Our results also lend increasing support to the idea that Verreaux's sifaka behavior can best be understood within a neighborhood framework. Sifaka group membership has been described as dynamic, with influxes of males during the mating season [Richard et al., 1974; Brockman, 1999; Lewis, 2004], wandering or roaming males [Richard et al., 1993; Kappeler et al., 2012], visiting males [Richard et al., 1993], and, as this study shows, even groups without resident males. Moreover, the absence of an impact of competitive

ability on entrance strategy suggests that the presumed link between competitive ability and physical characteristics such as body mass and weaponry may overlook important alternative behavioral strategies, such as coalitions. Finally, intraspecific differences in dispersal patterns exist, perhaps due to variation in habitat, predation levels, and demography.
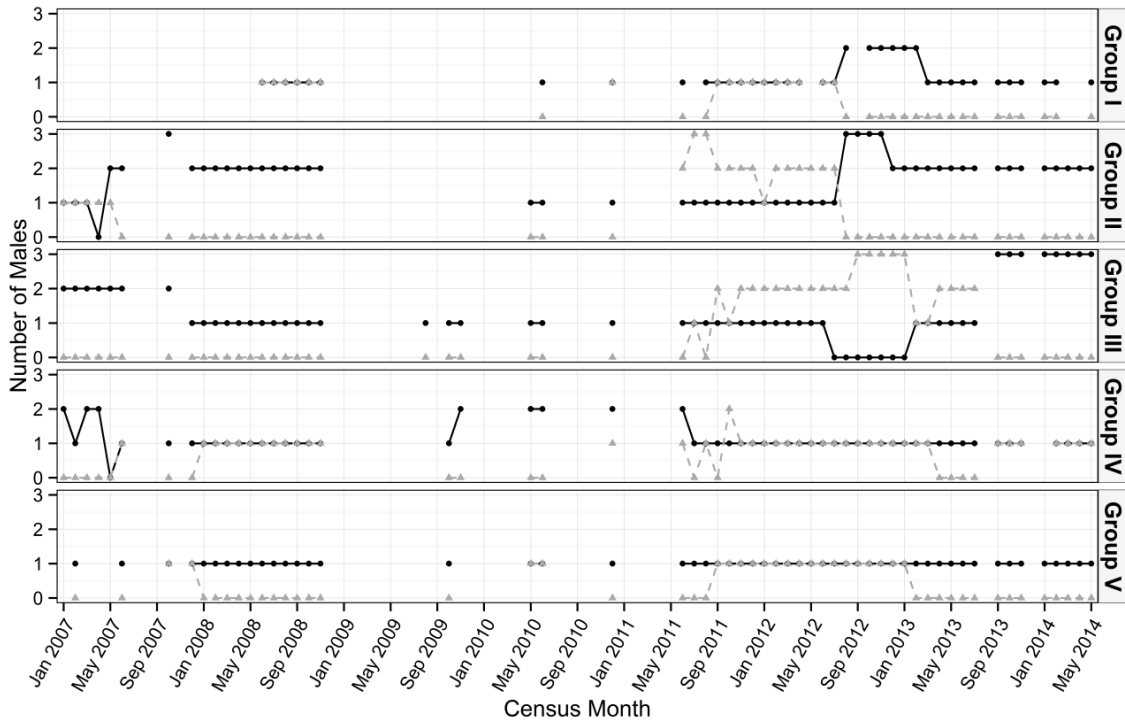
Fig. 1. Number of subadult and adult males in five study groups from January 2007 through May 2014. Missing data are indicated by gaps. Subadults = light triangles, dashed line. Adults = dark circles, solid line.
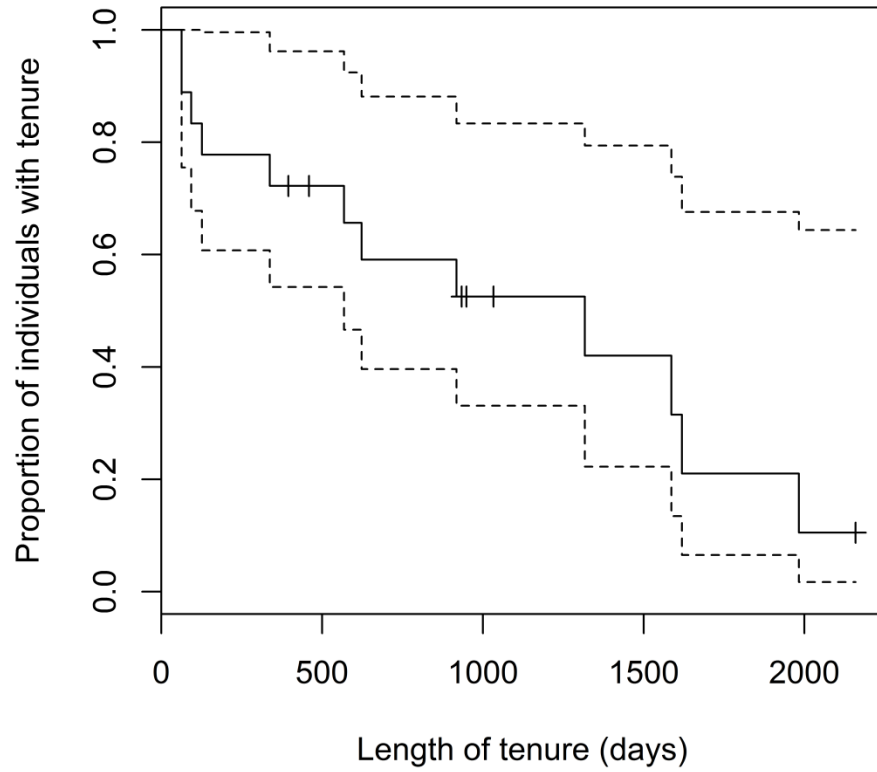
Fig. 2. Survival curve of alpha male tenure length. Estimate of median tenure is 1317 days (3.6 years) based on 18 males. Short vertical lines represent right-censored observations.
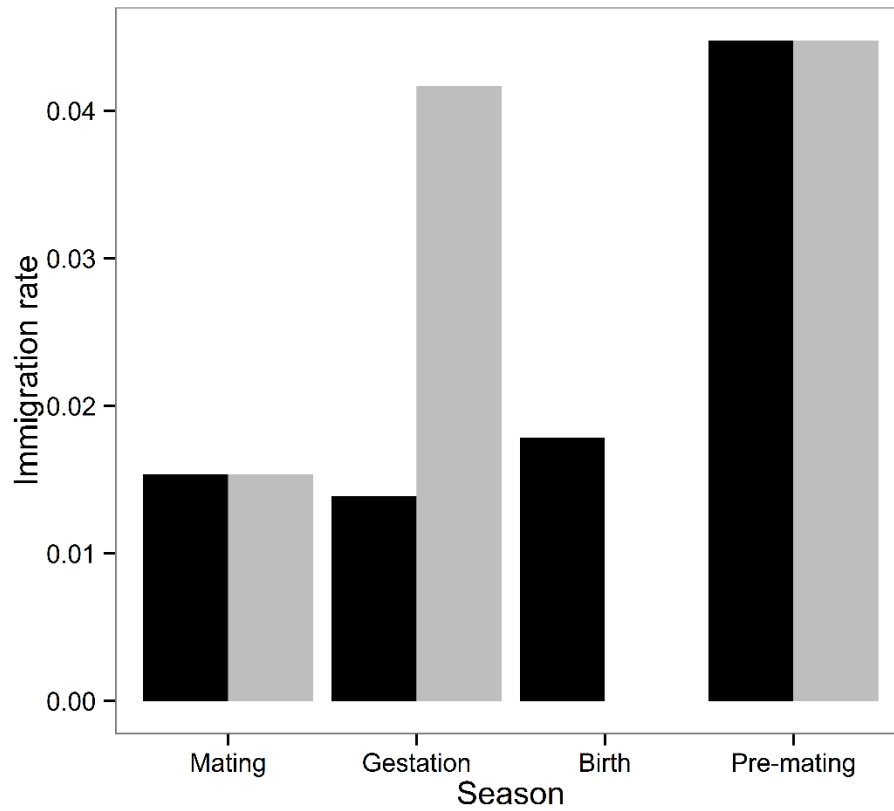
Fig. 3. Seasonal distribution of male immigrations for which data were of monthly resolution or less (N=13). Black bars represent subadults, and grey bars represent adults. Per-season immigration rate was calculated by dividing the number of immigrations in each season by the corresponding number of monthly census dates in that season.
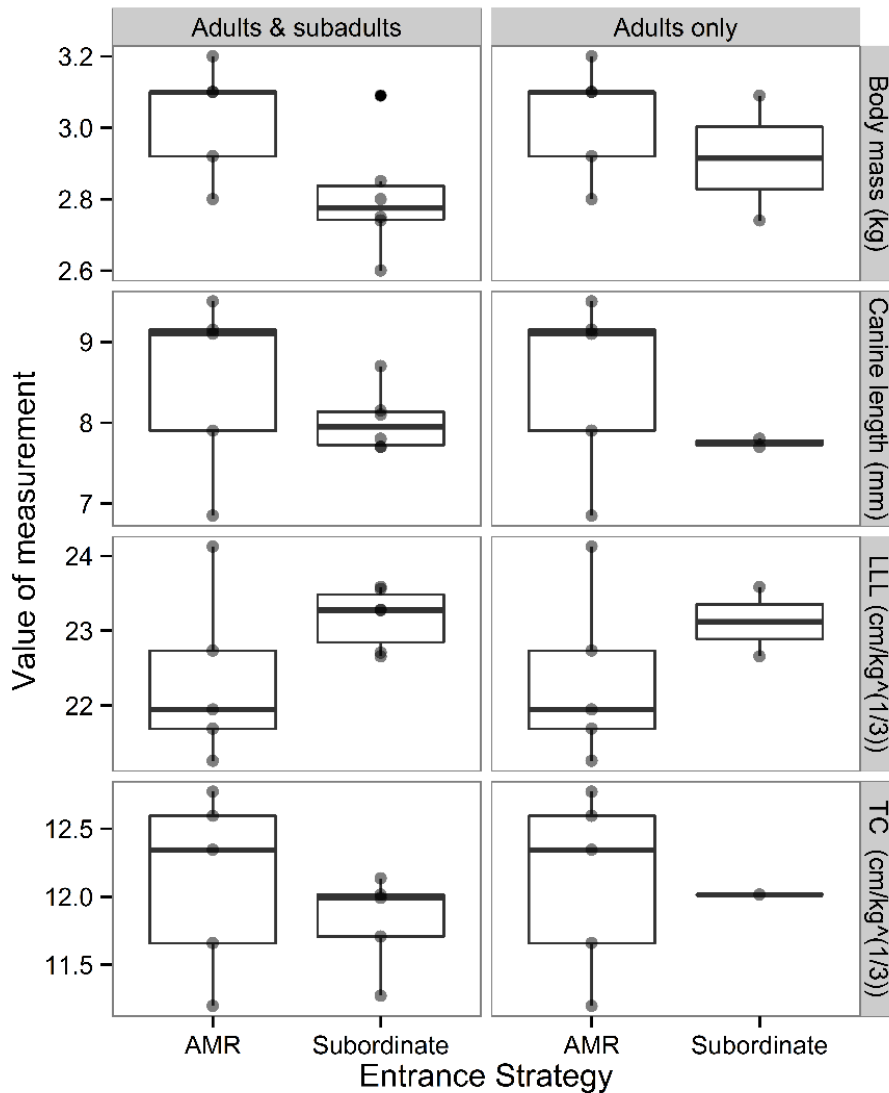
Fig. 4. Comparisons of morphological measurements from individuals employing different entrance strategies. AMR=Alpha male replacement, LLL=Lower limb length, TC=Thigh circumference. Left column includes individuals of all age classes (N_{AMR}=5 individuals, $N_{Subordinate}$=5-6 individuals). Points for each individual are overlaid with the boxplots. Right column includes adults only (N_{AMR}=5 individuals, $N_{Subordinate}$=1-2 individuals). Lines of box represent first, second, and third quartiles. Whiskers extend from the third quartile to the highest measurements within 1.5 times the interquartile range (IQR) and from the first quartile to the lowest measurements within 1.5 times the IQR. Note that more overlap in body mass between entrance strategies occurs when subadults are included.
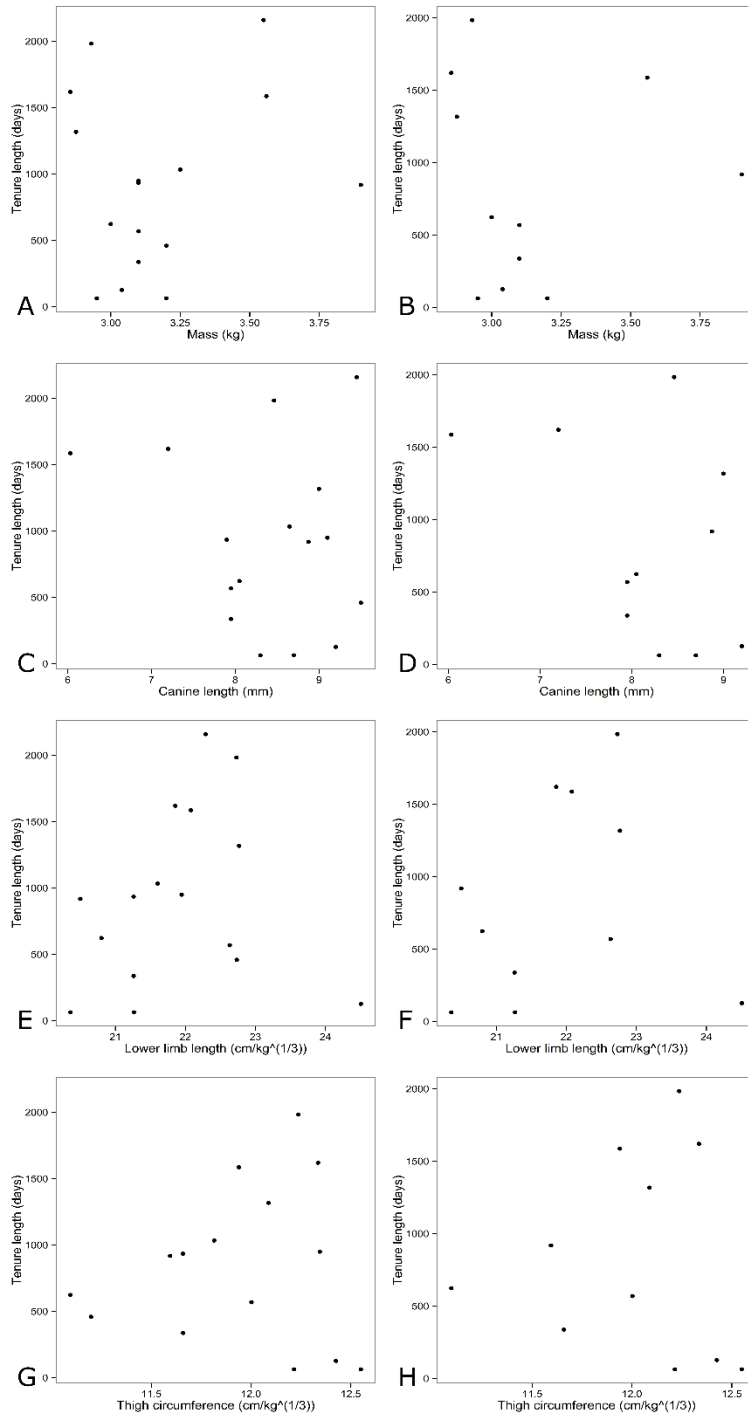
Fig. 5. Alpha male tenure lengths plotted against body mass (A, B), canine size (C, D), lower limb length (E, F), and thigh circumference (G, H). Each plot in the left column includes right-censored tenure lengths, which have been omitted in the adjacent column. $N_{A,C,E} = 16$; $N_G=15$; $N_{B,D,F,H}=11$

Table 1. Group composition and sampling effort for the five main study groups at Kirindy Mitea National Park, January 2007 through May 2014.

Group	Mean group size	Number of monthly censuses	Number of years of census data
I	5.0	35	2.9
II	6.5	58	4.8
III	7.3	59	5.0
IV	7.4	57	4.8
V	4.9	52	4.3
Overall	6.2	261	21.8

Group size includes individuals of all age classes. Summing the number of monthly censuses for each group yields 261 group-months. "Number of years of census data" is the number of monthly censuses divided by 12. Summing the years of census data for each group yields 21.8 group-years.

Table 2. Summary of mixed effects logistic regression modeling the timing of immigration.

Coefficient	Estimate	Std Error	Z	P
Intercept	-2.40	1.04	-2.30	0.02
Mating	0.79	1.30	0.61	0.54
Gestation	1.71	1.21	1.41	0.16
Pre-mating	2.40	1.19	2.01	0.05

Coefficients remain in logit space. Coefficient estimates are relative to the intercept "estimate", which represents the birth season. Subjects are Verreaux's sifaka (N=12) at Kirindy Mitea National Park.

Table 3. Spearman's rank correlations for each morphological measure of competitive ability.

Measurement	Rho	*P*	N	Rho*	*P**	N*
Body mass	-0.008	0.98	16	-0.320	0.34	11
Canine length	-0.096	0.72	16	-0.288	0.39	11
LLL	0.295	0.27	16	0.328	0.32	11
TC	-0.018	0.95	15	-0.182	0.59	10

LLL=Lower limb length, TC=Thigh circumference. Asterisks indicate analyses in which individuals with right-censored tenures were omitted.

Table 4. Selection of groups by subadult immigrants

Female availability measure	N immigrants	Percent of immigrants choosing most favorable FA	Percent of immigrants avoiding least favorable FA	Mean number groups compared	Mean number groups with identical FA	Mean difference between most and least favorable FA
AF	6	100%	100%	4.33	3	1.2 females
AF+SUBF	4	100%	100%	4.5	2.5	1.8 females
AM:AF	5	100%	100%	4	2.2	SR 2.2 times better
AM:(SUBF+AF)	6	100%	100%	4	2.2	SR 1.9 times better

FA=Female availability. SR=Sex ratio. The number of groups compared for each immigrant varied because complete demographic data were rarely available for all five groups around the time of immigration. This variation is reflected in the column labeled "Mean number of groups compared". Note that because some of the groups being compared often had identical FA, "choosing highest" and "avoiding lowest" refer to choosing/avoiding a maximum or minimum *value*, which may not be unique to the chosen *group*. Comparisons between groups were not made when no variation in FA existed.

Table 5. Comparison of pre-transfer and post-transfer groups for adult immigrants

Female availability measure	N immigrants	Percent of immigrants joining group with more favorable FA than previous group	Mean difference between most and least favorable FA
AF	3	67%	1 female
AF+SUBF	3	67%	1 female
AF:AM	3	100%	SR 1.5 times better*
(AF+SUBF):AM	3	100%	SR 1.5 times better*

FA=Female availability. SR=Sex ratio. Asterisk indicates that the SR comparison only applies to the one immigrant that joined a group that had an alpha male around the time of immigration. In the two other cases, immigrants joined groups with alpha male vacancies (SR=0).

References

Alberts SC, Altmann J. 1995. Balancing costs and opportunities: dispersal in male baboons. American Naturalist 145:279–306.

Bates D, Maechler M, Bolker B, Walker B. 2014. lme4: Linear mixed-effects models Using Eigen and S4. R package version 1.1-5. URL: http://CRAN.Rproject.org/package=lme4.

Bayart F, Simmen B. 2005. Demography, range use, and behavior in black lemurs (*Eulemur macaco macaco*) at Ampasikely, northwest Madagascar. American Journal of Primatology 67:299–312.

Bengtsson BO. 1978. Avoiding inbreeding: at what cost? Journal of Theoretical Biology 73:439-444.

Boelkins RC, Wilson AP. 1972. Intergroup social dynamics of the Cayo Santiago rhesus (*Macaca mulatta*) with special reference to changes in group membership by males. Primates 13:125–139.

Bonte D, Van Dyck H, Bullock JM, et al. 2012. Costs of dispersal. Biological Reviews 87:290-312.

Borries C. 2000. Male dispersal and mating season influxes in Hanuman langurs living in multi-male groups. Kappeler PM, editor. Primates males: Causes and consequences of variation in group composition. Cambridge: Cambridge University Press. p 146–158.

Brockman DK. 1999. Reproductive behavior of female *Propithecus verreauxi* at Beza Mahafaly, Madagascar. International Journal of Primatology 20:375–398.

Brockman DK, Whitten PL, Richard AF, Benander B. 2001. Birth season testosterone levels in male Verreaux's sifaka, *Propithecus verreauxi*: insights into socio-demographic factors mediating seasonal testicular function. Behavioral Ecology and Sociobiology 49:117–127.

Cheney DL, Seyfarth RM. 1983. Nonrandom dispersal in free-ranging vervet monkeys: social and genetic consequences. American Naturalist 122:392–412.

Clarke PMR, Henzi SP, Barrett L, Rendall D. 2008. On the road again: competitive effects and condition dependent dispersal in male baboons. Animal Behaviour 76:55–63.

Clobert J, Le Galliard J-F, Cote J, Meylan S, Massot M. 2009. Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. Ecology Letters 12:197–209.

Clutton-Brock TH. 1989. Female transfer and inbreeding avoidance in social mammals. Nature 337:70–72.

Cole EF, Quinn JL. 2012. Personality and problem-solving performance explain competitive ability in the wild. Proceedings of the Royal Society B 279:1168–1175.

Cords M. 2002. When are there influxes in blue monkey groups? In: Glenn ME, Cords M, editors. The guenons: Diversity and adaptation in African monkeys. New York: Kluwer Academic/Plenum Publishers. p 189-201.

Crockett CM, Sekulic R. 1984. Infanticide in red howler monkeys (*Alouatta seniculus*).

In: Hausfater G, Hrdy SB, editors. Infanticide: Comparative and Evolutionary

Perspectives. New York: Aldine. p 173-191.

Danchin E, Heg D, Doligez B. 2001. Public information and breeding habitat selection.

In: Clobert J, Danchin E, Dhondt AA, Nichols JD, editors. Dispersal. New York:

Oxford University Press. p 243-258.

Dobson F. 1982. Competition for mates and predominant juvenile male dispersal in

mammals. Animal Behaviour 30:1183–1192.

Drickamer LC, Vessey SH. 1973. Group changing in free-ranging male rhesus monkeys.

Primates 14:359–368.

Fedigan LM, Jack KM. 2004. The demographic and reproductive context of male

replacements in *Cebus capucinus*. Behaviour 141:755–775.

Gandon S, Michalakis, Y. 2001. Multiple causes of the evolution of dispersal. In: Clobert

J, Danchin E, Dhondt AA, Nichols JD, editors. Dispersal. New York: Oxford

University Press. p 155-167.

Greenwood PJ, Harvey PH. 1982. The natal and breeding dispersal of birds. Annual

Review of Ecology and Systematics 13:1–21.

Greenwood PJ. 1980. Mating systems, philopatry and dispersal in birds and mammals.

Animal Behaviour 28:1140–1162.

Hamilton WD. 1967. Extraordinary sex ratios. Science 156:477–488.

Harding RSO, Olson DK. 1986. Patterns of mating among male patas monkeys

(*Erythrocebus patas*) in Kenya. American Journal of Primatology 11:343–358.

Henzi SP, Lucas JW. 1980. Observations on the intertroop movement of adult vervet

monkeys (*Cercopithecus aethiops*). Folia Primatologica 33:220–235.

Hurlbert SH. 1984. Pseudoreplication and the design of ecological field experiments. Ecological Monographs 54:187–211.

Isbell LA, Cheney DL, Seyfarth RM. 1990. Costs and benefits of home range shifts among vervet monkeys (*Cercopithecus aethiops*) in Amboseli National Park, Kenya. Behavioral Ecology and Sociobiology 27:351–358.

Isbell LA, Cheney DL, Seyfarth RM. 1993. Are immigrant vervet monkeys, *Cercopithecus aethiops*, at greater risk of mortality than residents? Animal Behaviour 45:729–734.

Isbell LA, Van Vuren D. 1996. Differential costs of locational and social dispersal and their consequences for female group-living primates. Behaviour 133:1–36.

Jack KM, Fedigan L. 2004a. Male dispersal patterns in white-faced capuchins, *Cebus capucinus* Part 1: patterns and causes of natal emigration. Animal Behaviour 67:761–769.

Jack KM, Fedigan L. 2004b. Male dispersal patterns in white-faced capuchins, *Cebus capucinus* Part 2: patterns and causes of secondary dispersal. Animal Behaviour 67:771–782.

Jolly A. 1966. Lemur behavior: a Madagascar field study. Chicago: University of Chicago Press.

Jolly A, Gustafson H, Oliver WL, O'Connor SM. 1982. *Propithecus verreauxi* population and ranging at Berenty, Madagascar, 1975 and 1980. Folia Primatologica 39:124–144.

Jones KC. 1983. Inter-troop transfer of *Lemur catta* males at Berenty, Madagascar. Folia Primatologica 40:145–160.

Kaplan EL, Meier P. 1958. Nonparametric estimation from incomplete observations. Journal of the American Statistical Association 53:457.

Kappeler PM, Fichtel C. 2012. A 15-year perspective on the social organization and life history of sifaka in Kirindy Forest. In: Kappeler PM, Watts DP, editors. Long-term field studies of primates. Berlin Heidelberg: Springer-Verlag. p 101–121.

Kappeler PM, Mass V, Port M. 2009. Even adult sex ratios in lemurs: Potential costs and benefits of subordinate males in Verreaux's sifaka (*Propithecus verreauxi*) in the Kirindy Forest CFPF, Madagascar. American Journal of Physical Anthropology 140:487–497.

Kappeler PM, Schäffler L. 2008. The lemur syndrome unresolved: extreme male reproductive skew in sifakas (*Propithecus verreauxi*), a sexually monomorphic primate with female dominance. Behavioral Ecology and Sociobiology 62:1007–1015.

Korstjens AH, Schippers EP. 2003. Dispersal patterns among olive colobus in Tai National Park. International Journal of Primatology 24:515–539.

Kraus C, Heistermann M, Kappeler PM. 1999. Physiological suppression of sexual function of subordinate males: a subtle form of intrasexual competition among male sifakas (*Propithecus verreauxi*)? Physiology & Behavior 66:855–861.

Kummer H, Goodall J. 1985. Conditions of innovative behaviour in primates.

Philosophical Transactions of the Royal Society B: Biological Sciences 308:203–214.

Kubzdela KS. 1997. Sociodemography in diurnal primates: the effects of group size and female dominance rank on intra-group spatial distribution, feeding competition, female reproductive success, and female dispersal patterns in white sifaka, *Propithecus verreauxi verreauxi* [Dissertation]. University of Chicago.

Lawler RR, Richard AF, Riley MA. 2003. Genetic population structure of the white sifaka (*Propithecus verreauxi verreauxi*) at Beza Mahafaly Special Reserve, southwest Madagascar (1992-2001). Molecular Ecology 12:2307–2317.

Lawler RR. 2006. Sifaka positional behavior: ontogenetic and quantitative genetic approaches. American Journal of Physical Anthropology 131:261–271.

Lawler RR. 2007. Fitness and extra-group reproduction in male Verreaux's sifaka: an analysis of reproductive success from 1989–1999. American Journal of Physical Anthropology 132:267–277.

Lawler RR, Richard AF, Riley MA. 2005. Intrasexual selection in Verreaux's sifaka (*Propithecus verreauxi verreauxi*). Journal of Human Evolution 48:259–277.

Leimberger KG, Lewis RJ. 2015. Determinants of primate sex ratios: an analysis of demography in Verreaux's sifaka (*Propithecus verreauxi*). [Meeting Abstract]. American Association of Physical Anthropologists.

Lewis RJ. 2004. Sources of variation in male-female relationships: Power, conflict, and cooperation [Dissertation]. Duke University.

Lewis RJ. 2005. Sex differences in scent-marking in sifaka: Mating conflict or male

services? American Journal of Physical Anthropology 128:389–398.

Lewis RJ. 2008. Social Influences on Group Membership in *Propithecus verreauxi verreauxi*. International Journal of Primatology 29:1249–1270.

Lewis RJ. 2009. Chest staining variation as a signal of testosterone levels in male Verreaux's Sifaka. Physiology & Behavior 96:586–592.

Lewis RJ, Kappeler PM. 2005. Seasonality, body condition, and timing of reproduction in *Propithecus verreauxi verreauxi* in the Kirindy Forest. American Journal of Primatology 67:347–364.

Lewis RJ, Rakotondranaivo F. 2011. The impact of Cyclone Fanele on sifaka body condition and reproduction in the tropical dry forest of western Madagascar. Journal of Tropical Ecology 27:429–432.

Lewis RJ, Razafindrasamba SM, Tolojanahary JP. 2003. Observed infanticide in a seasonal breeding prosimian (*Propithecus verreauxi verreauxi*) in Kirindy Forest, Madagascar. Folia Primatologica 74:101–103.

Lewis RJ, van Schaik CP. 2007. Bimorphism in male Verreaux's sifaka in the Kirindy Forest of Madagascar. International Journal of Primatology 28:159–182.

Lindburg DG. 1969. Rhesus monkeys: Mating season mobility of adult males. Science 166:1176-1178.

Littlefield BL. 2010. Infanticide following male takeover event in Verreaux's sifaka (*Propithecus verreauxi verreauxi*). Primates 51:83–86.

Machlis L, Dodd PWD, Fentress JC. 1985. The pooling fallacy: problems arising when

individuals contribute more than one observation to the data set. Zeitschrift für Tierpsychologie 68:201–214.

Marsh CW. 1979. Female transference and mate choice among Tana River red colobus. Nature 281:568–569.

Mass V, Heistermann M, Kappeler PM. 2009. Mate-guarding as a male reproductive tactic in *Propithecus verreauxi*. International Journal of Primatology 30:389–409.

Mitchell CL. 1994. Migration alliances and coalitions among adult male South American squirrel monkeys (*Saimiri sciureus*). Behaviour 130:169–190.

Moore J, Ali R. 1984. Are dispersal and inbreeding avoidance related? Animal Behaviour 32:94-112.

Morelli TL, King SJ, Pochron ST, Wright PC. 2009. The rules of disengagement: takeovers, infanticide, and dispersal in a rainforest lemur, *Propithecus edwardsi*. Behaviour 146:499–523.

Nagy H. 2007. A preliminary analysis of Verreaux's sifaka habitat in Kirindy Mitea National Park, Madagascar. [Master's Thesis]. Duke University.

Norscia I, Carrai V, Borgognini-Tarli SM. 2006. Influence of Dry Season and Food Quality and Quantity on Behavior and Feeding Strategy of *Propithecus verreauxi* in Kirindy, Madagascar. International Journal of Primatology 27:1001–1022.

Packer C. 1979. Inter-troop transfer and inbreeding avoidance in *Papio anubis*. Animal Behaviour 27:1–36.

Pope TR. 1990. The reproductive consequences of male cooperation in the red howler monkey: paternity exclusion in multi-male and single-male troops using genetic

markers. Behavioral Ecology and Sociobiology 27:439–446.

Port M, Johnstone RA, Kappeler PM. 2012. The evolution of multimale groups in
Verreaux's sifaka, or how to test an evolutionary demographic model. Behavioral
Ecology: 889–897.

Pusey AE, Packer C. 1987. Dispersal and philopatry. In: Smuts BB, Cheney CL, Seyfarth
RM, Wrangham RW, Struhsaker TT, editors. Primate Societies. Chicago:
University of Chicago Press. p 250-266.

R Core Development Team. 2014. R: A language and environment for statistical
computing. R Foundation for Statistical Computing, Vienna, Austria. URL
http://www.Rproject.org/.

Reader SM, Laland KN. 2001. Primate innovation: sex, age and social rank differences.
International Journal of Primatology 22:787–805.

Richard AF. 1974. Intraspecific variation in social organization and ecology of
Propithecus verreauxi. Folia Primatologica 22:178–207.

Richard AF. 1985. Social boundaries in a Malagasy prosimian, the Sifaka (*Propithecus
verreauxi*). International Journal of Primatology 6:553–568.

Richard AF. 1992. Aggressive competition between males, female-controlled polygyny
and sexual monomorphism in a Malagasy primate, *Propithecus verreauxi*. Journal
of Human Evolution 22:395–406.

Richard A, Nicoll M. 1987. Female Social Dominance and Basal Metabolism in a
Malagasy Primate, *Propithecus verreauxi*. American Journal of Primatology
12:309–314.

Richard A, Rakotomanga P, Schwartz M. 1991. Demography of *Propithecus verreauxi* at

    Beza Mahafaly, Madagascar: Sex Ratio, Survival, and Fertility, 1984-1988.

    American Journal of Physical Anthropology 84:307–322.

Richard AF, Rakotomanga P, Schwartz M. 1993. Dispersal by *Propithecus verreauxi* at

    Beza Mahafaly, Madagascar: 1984–1991. American Journal of Primatology 30:1–

    20.

Richard AF, Dewar RE, Schwartz M, Ratsirarson J. 2002. Life in the slow lane?

    Demography and life histories of male and female sifaka (*Propithecus verreauxi*

    verreauxi). Journal of Zoology 256:421–436.

Riebli T, Avgan B, Bottini A-M, et al. 2011. Behavioural type affects dominance and

    growth in staged encounters of cooperatively breeding cichlids. Animal

    Behaviour 81:313–323.

Sapolsky RM, Ray JC. 1989. Styles of dominance and their endocrine correlates among

    wild olive baboons (*Papio anubis*). American Journal of Primatology 18:1–13.

Schoof VAM, Jack KM, Isbell LA. 2009. What traits promote male parallel dispersal in

    primates? Behaviour 146:701–726.

Simmen B, Tarnaud L, Hladik A. 2012. Leaf nutritional quality as a predictor of primate

    biomass: further evidence of an ecological anomaly within prosimian

    communities in Madagascar. Journal of Tropical Ecology 28:141–151.

Smale L, Nunes S, Holekamp KE. 1997. Sexually dimorphic dispersal in mammals:

    Patterns, causes, and consequences. Advances in the Study of Behavior, Vol 26

    26:181–250.

Smith EO. 1992. Dispersal in sub-Saharan baboons. Folia Primatologica 59:177–185.

Sommer V, Rajpurohit L. 1989. Male Reproductive Success in Harem Troops of Hanuman Langurs (*Presbytis entellus*). International Journal of Primatology 10:293–317.

Sprague DS, Suzuki S, Takahashi H, Sato S. 1998. Male life history in natural populations of Japanese macaques: Migration, dominance rank, and troop participation of males in two habitats. Primates 39:351–363.

Sprague DS. 1992. Life history and male intertroop mobility among Japanese macaques (*Macaca fuscata*). International Journal of Primatology 13:437–454.

Strier KB. 1994. Myth of the typical primate. Yearbook of Physical Anthropology 37:233–271.

Sussman RW. 1992. Male life history and intergroup mobility among ringtailed lemurs (*Lemur catta*). International Journal of Primatology 13:395–413.

Sussman RW, Richard AF, Ratsirarson J, et al. 2012. Beza Mahafaly Special Reserve: Long-Term Research on Lemurs in Southwestern Madagascar. In: Kappeler PM, Watts DP, editors. Long-Term Field Studies of Primates. Berlin Heidelberg: Springer-Verlag. p 45–66.

Therneau T. 2014. A package for survival analysis in S. R package version 2.37-7, URL: http://CRAN.R-project.org/package=survival.

Teichroeb JA, Wikberg EC, Sicotte P. 2009. Female dispersal patterns in six groups of ursine colobus (Colobus vellerosus): infanticide avoidance is important. Behaviour 146:4–5.

Teichroeb JA, Wikberg EC, Sicotte P. 2011. Dispersal in male ursine colobus monkeys (*Colobus vellerosus*): influence of age, rank and contact with other groups on dispersal decisions. Behaviour 148:765–793.

van Hooff JARAM. 2000. Relationships among non-human primate males: a deductive framework. In: Kappeler PM, editor. Primate Males: causes and Consequences of Variation in Group Composition. Cambridge: Cambridge University Press. p 183–191.

van Noordwijk MA, van Schaik CP. 1985. Male migration and rank acquisition in wild long tailed macaques (*Macaca fascicularis*). Animal Behaviour 33:849–861.

van Noordwijk MA, van Schaik CP. 2001. Career moves: Transfer and rank challenge decisions by male long-tailed macaques. Behaviour 138:359–395.

van Schaik CP, Brockman DK. 2005. Seasonality in primate ecology, reproduction and life history: an overview. In: Brockman DK, van Schaik CP, editors. Seasonality in primates. New York: Cambridge University Press. p 3-20.

Verbeek MEM, Boon A, Drent PJ. 1996. Exploration, aggressive behaviour an dominance in pair-wise confrontations of juvenile male great tits. Behaviour 133:945–963.

Ward AJW, Thomas P, Hart PJB, Krause J. 2004. Correlates of boldness in three-spined sticklebacks (*Gasterosteus aculeatus*). Behavioral Ecology and Sociobiology 55:561–568.

Wolff JO, Lundy KI, Baccus R. 1988. Dispersal, inbreeding avoidance and reproductive success in white-footed mice. Animal Behaviour 36:456–465.