Behav Ecol Sociobiol (2001) 49:117–127

ORIGINAL ARTICLE

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# Birth season testosterone levels in male Verreaux's sifaka, *Propithecus verreauxi*: insights into socio-demographic factors mediating seasonal testicular function

Received: 22 November 1999 / Revised: 27 April 2000 / Accepted: 15 October 2000

**Abstract** Previous research suggests that although reproduction and testicular function in wild sifaka (*Propithecus verreauxi*) are highly seasonal, birth season elevations in fecal testosterone (T) in transferring males indicate that social factors may be as important as climatic factors in regulating reproductive function in sifaka. This paper examines the relationship of male dispersal and social status to the patterning of birth season aggression and testicular function in *P. verreauxi* at Beza Mahafaly Special Reserve, Madagascar. Behavioral and hormonal data were collected from a total of 38 adult males, 15 residing in seven stable groups and 23 living in eight unstable groups, yielding 186 fecal samples and 493 focal animal hours of observation. The results suggest that birth season elevations in fecal testosterone are the consequence of social disruption resulting from male movements between groups and the particular responses of individual males to dispersal events. Hormonal responses to dispersal events appear to precede behavioral responses and occasionally register reactions not concomitantly evident in the behavioral response, and may be predictive of future events. Hormonal reactions occurred primarily in resident alpha males, suggesting that they differ in their assessment of destabilizing influences, perhaps due to different reproductive opportunities and/or investment. These findings are important for the new insights they provide into the role of androgens in mediating male dispersal, life history, and reproductive strategies, and suggest that investigations of androgen-behavior interactions in free-ranging populations can be a powerful new tool for assessing the contextual and motivational basis of social behavior.

**Keywords** Sifaka · Testosterone · Seasonality · Transfer · Aggression

## Introduction

Selection for optimal timing of reproductive events has favored the evolution of seasonal reproduction in most vertebrates (Crews 1992). As might be expected from their different reproductive strategies, males and females often differ in sensitivity to the proximal cues that regulate seasonal reproduction (Lindburg 1987; Bronson 1989). Seasonal changes in male reproductive capacity vary considerably across vertebrate species, ranging from complete regression of the testes (<10% of maximum weight) and suppression of testosterone (T) to minimal regression and maintenance of elevated T (Lincoln 1981; Wingfield et al. 1990).

Associated differences in species-specific mating systems and reproductive strategies suggest that the seasonal patterning of T secretion reflects evolutionary tradeoffs between the reproductive benefits and costs of aggression and other aspects of reproductive effort (Wingfield et al. 1990). Data showing that serum T parallels rates of aggression more closely than sexual behavior have led to the formulation of the "challenge hypothesis" (Wingfield et al. 1990, 833), which posits that the "frequency or intensity of reproductive aggression as an effect of T is strongest in situations of social instability, such as during the formation of dominance relationships, the establishment of territorial boundaries, or challenges by a conspecific male for territory or access to mates". Additionally, prolonged elevations in T are expected to occur in nonparental (e.g., polygnous) males

Communicated by P.M. Kappeler

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whereas low T concentrations are predicted for parental (e.g., monogamous) males (Wingfield et al. 1990). Supporting this hypothesis is the evidence in birds (Wingfield 1994) and primates (Sapolsky 1983, 1993) that T has a more consistent relationship with aggression or rank during social disruption than during periods of social stability. T has also been shown to regulate mating challenges as well as mate defense. T implants stimulate acquisition of additional mates in normally monogamous birds (Wingfield 1994) and induce home range expansion and immigration in female voles (Taitt and Krebs 1982). However, seasonal elevations in endogenous T do not appear to activate dispersal in Belding's ground squirrels (Holekamp et al. 1984) or spotted hyenas (Holekamp and Smale 1998). Few studies have examined the relationship of hormones to mating challenges in primates, but elevated T levels were observed in an immigrant male baboon (Alberts et al. 1992) whereas abnormally low T was associated with failure of immigration attempts in a unilaterally cryptorchid baboon male (Altmann et al. 1992). Home range expansion follows seasonal testicular enlargement in Coquerel's mouse lemurs (Kappeler 1997).

Data on the costs of T are somewhat contradictory. T implants in several bird species have been associated with loss of body fat, increased stress, delayed molt, impaired or increased survival, and suppression of paternal behavior (Wingfield et al. 1990; Ketterson and Nolan 1992). More studies in a wider range of species are needed to more adequately define the costs and benefits of seasonal patterns of T secretion and test their relationship to mating systems and reproductive strategies.

Although seasonal variation in T secretion has been reported for a number of mammals (Lincoln 1981), including primates (reviewed in Strier et al. 1999), only a handful of studies have investigated androgen-behavior interactions and their social influences in free-ranging populations (Holekamp et al. 1984; Sapolsky 1986; Brockman et al. 1998; Holekamp and Smale 1998; Kraus et al. 1999; Strier et al. 1999). The objective of this study was to investigate the factors regulating male testicular function in wild Verreaux's sifaka (*Propithecus verreauxi*), a diurnal strepsirrhine primate from south and southwest Madagascar (Tattersall 1982). Sifaka reproduction is highly seasonal, with 96% of births occurring during July and August (Richard and Dewar 1991; unpublished data). Thus, seasonality of testicular function in sifaka would be expected to resemble that observed in other strictly seasonal mammals (e.g., rock hyrax: Neaves 1973; red deer: Lincoln 1971; pipistrelle bat: Racey and Tam 1974), including some strepsirrhines (Whitten and Brockman, in press). Hormonal studies show that while testicular function in sifaka is broadly seasonal (Brockman et al. 1998; Kraus et al. 1999), there appears to be no *statistically* significant seasonal effect on weekly mean fecal testosterone (fT) levels in adult males (but see Kraus et al. 1999). This is a consequence of marked birth season elevations in fT in transferring and solitary males and in males residing in unstable groups (Brockman et al. 1998). These results suggest that seasonal fluctuations in fT may be dampened by social disruption and dispersal during the birth season, and that sociodemographic factors are as important as climatic factors in regulating male reproductive function in this species.

Generally, male sifaka are the dispersing sex, most often leaving their natal group at 3 years of age (Richard et al. 1993, unpublished data; Kubzdela 1997). Male group tenure averages 5 years, but younger males (3–5 years of age) transfer two to three times more frequently between groups than do older males (>6 years old) (Richard et al. 1993) and some males move as often as twice a year. Approximately 35% of adult males transfer annually and a third of these transfers occur during the birth season, so that as many as 60% of groups undergo a change in male membership at this time (Brockman and Whitten 1999; K.S. Kubzdela, unpublished data). These changes can destabilize groups and threaten male status by increasing male-male aggression within groups and the peripheralization of resident males. Moreover, reports of occasional transfer-related infanticides (Richard et al., unpublished data) suggest that some transferring males also pose a risk to neonates. The fitness implications of these results for sifaka are currently being investigated (R. Lawler, unpublished data), but aggression-related dispersal during the birth season may be one of several male tactics, including perhaps infanticide, to enhance future mating opportunities. Male infanticide has been observed in a number of mammalian taxa (reviewed in van Schaik and Janson 2000), including strepsirrhines (Jolly et al. 2000), but its role as a reproductive tactic in *Propithecus* (Wright 1995; Erhart and Overdorff 1998; Richard et al., unpublished data) has yet to be demonstrated.

The costs to sifaka males of maintaining extra-breeding season elevations in fT are unknown, but the benefits of androgen-mediated aggression during the birth season may include greater transfer success and increased mating opportunities the following mating season for immigrating males and the defense of group tenure and offspring for resident males. Here we report the results from the first field season of an on-going 5-year study on the social and reproductive significance of birth season elevations in fT in sifaka at Beza Mahafaly Special Reserve (BMSR), Madagascar. We hypothesized that transfer attempts would be associated with elevated fT levels in adult immigrants, in resident alpha males defending their groups, and in fathers defending newborn infants. We predicated that fT would be (1) higher in transferring or visiting males than in residents; (2) higher in alpha males than in subordinates, (3) higher in males residing in groups with infants than in those groups without infants, (4) higher in males living in unstable than in stable groups, and (5) higher in males who were aggressive during transfer.

## Methods

### Subjects

The study focused on 200 (102 males, 98 females) marked and habituated *P. verreauxi* in sector 1 (100 ha) of BMSR during the peak July–August 1998 birth season. Individuals were identified via colored collars, uniquely shaped and numbered tags, and correspondingly numbered ear notches. The subject of long-term demographic research (Richard et al. 1991, 1993), the study population has been censused annually from 1984 to 1992 and thereafter at monthly intervals by local BMSR staff, who record births, deaths, and migration. Daily monitoring of groups during the birth season provides birth dates (and perinatal mortality rates) and these in conjunction with morphometric data, yield estimates of age for 370 marked sifaka (Richard et al. 1991, 1993; unpublished data). These data and previous observations of mating (Richard 1974, 1992; Brockman et al. 1998) indicate that although most 1.5-year-old juvenile males have fully descended testes and 4-year-old subadult males successfully compete for mating opportunities, males (and females) do not achieve adult body mass until the end of the 5th year when long-bone growth ceases (Richard et al., in press). The April 1998 census of sector 1 identified 30 social groups ranging in size from 1 to 12 marked individuals living within the protected area (A.F. Richard, unpublished data). Twenty-five of these groups contained adult males over 6 years of age and 14 contained two to three such males. New groups form and are subsequently named (e.g., Andafy, Celeste, Kashka) when nulliparous young adult females disperse from predominately large natal groups (Richard et al., unpublished data) or when new females immigrate into the reserve and establish their home ranges.

### Focal groups and male residence

Between late June and mid-August, we used a trail grid (50 m$^2$) to census 30 groups (four total censuses), recording births and changes in adult group composition. During the census period, 8 of the surveyed groups were identified as “unstable,” defined as having experienced a transfer event within the previous 1–6 weeks, including recruitment of males during female home range boundary disputes, male eviction, or the formation of a new group. Eighteen of the surveyed groups contained newborn infants.

Seven groups were sampled intensively and eight additional groups were sampled opportunistically. Five unstable groups and two stable groups (one of which became unstable during the course of the study) were observed and sampled for 7–10 days. Six stable and two unstable groups were sampled among the opportunistic groups. Behavioral and hormonal data were collected from a total of 38 adult males, 15 residing in seven stable groups and 23 adult males living in eight unstable groups (Table 1). Nineteen of these focal males were identified as *residents* who had not migrated since the April 1998 census; 12 were *immigrants* who had transferred into new groups since the April 1998 census, and 7 were *visitors* who non-aggressively entered a neighboring group for 0.5–2 days without making a change in residence (Richard et al. 1993). Four resident males were peripheralized during the study, having been displaced by new immigrants or aggressively evicted from their resident groups. Nine of the sampled groups contained a new infant and seven were without infants at the time of sampling (Table 1).

### Data collection and analysis

Data from opportunistically sampled groups were collected during the 6-day biweekly census periods when resident males were observed voiding. Continuous and ad libitum sampling methods were used to collect data on male movements and on submissive and aggressive interactions. Daily focal animal follows (Altmann 1974) and associated fecal samples were collected on 23 males distributed among the seven intensively sampled groups, averaging 25.97±2.3 (SE) focal animal hours per male. Observations began at 0900 hours when the animals awakened and terminated at 1500–1700 hours when they retired, yielding 493 h of focal re-

**Table 1** Social groups and males sampled, June–August 1998 (*Identification number* of sexually mature males sampled; *Unstable groups* instability indicated by male immigration/eviction, female group takeover, and new group formation; *asterisks* indicate intensively sampled groups)

| Stable groups | Identification number | Number of fecal samples collected | Number of sexually mature females | Infants | Unstable groups | Identification number | Number of fecal samples collected | Number of sexually mature females | Infants |
|---|---|---|---|---|---|---|---|---|---|
| Chocolat* | 9060 | 7 | 2 | 1 | Andafy* | 203 | 8 | 3 | 3 |
| | 263 | 7 | | | | 160 | 7 | | |
| Enafa | 177 | 1 | 2 | 1 | | 9031 (visiting) | 1 | | |
| Fanondrovery | 212 | 1 | 4 | 2 | Celeste | 143 | 1 | 1 | 1 |
| | 173 | 1 | | | | 9106 (visiting) | 1 | | |
| Fotaka | 118 | 1 | 3 | 2 | Pap-D* (early July) | 114 | 8 | 1 | 0 |
| | 9119 | 1 | | | | 239 | 8 | | |
| Kashka | 189 | 1 | 2 | 1 | | 216 | 7 | | |
| | 9025 | 2 | | | Rabingy* (late July) | 114 | 7 | 1 | 0 |
| Vamba | 213 | 1 | 2 | 1 | | 239 | 7 | | |
| | 145 | 1 | | | | 216 | 7 | | |
| Zavmad | 218 | 2 | 4 | 1 | | 257 (peripheral) | 3 | | |
| Vaovao* (became unstable) | 243 | 7 | 4 | 0 | | 42 (peripheral) | 2 | | |
| | 9003 | 6 | | | Rengor* | 211 | 9 | 1 | 0 |
| | 9006 | 5 | | | | 9 | 10 | | |
| | | | | | | 9021 | 4 | | |
| | | | | | | 9146 | 4 | | |
| | | | | | Sylvia | 258 | 1 | 1 | 0 |
| | | | | | | 68 | 1 | | |
| | | | | | Tsyemelia* | 282 | 8 | 2 | 0 |
| | | | | | | 92 | 6 | | |
| | | | | | | 294 | 12 | | |
| | | | | | | 9096 (visiting) | 3 | | |

cords. Alpha-subordinate positions were determined based upon consistent direction and outcome of aggressive (supplants, cuffs, grabs, bites, fights; Brockman 1994) and submissive (fear-chatter/grimace) behavior. Alpha males were predicted to only receive submissive gestures and to be the sole initiator/winners of aggression, while subordinates were those who fear-chattered/grimaced and were the recipients/losers of aggressive encounters (Brockman et al. 1998). Behavioral and hormonal analysis of rank effects was confined to the 15 groups in which alpha-subordinate positions could be determined. Paired *t*-tests were used in within-group alpha/subordinate comparisons to reduce the effects of inter-group differences. Interactions between significant fT-related variables (e.g., rank and group stability) were tested using two-way ANOVAs, with significance set at *P*=0.05. Data are reported as means±SE.

Daily morning fecal samples were collected from each resident/immigrant/peripheral adult male (and female) in the selected groups for 7–10 days, yielding a total of 186 samples, including 18 collected from 7 females (Table 1). Averages of 6.54±0.48 samples/male (*n*=24 males) were collected in intensively sampled groups and 1.14±0.1 samples/male were collected in the opportunistically (n=14 males) sampled groups. Fecal samples were packaged and preserved as previously described (Brockman et al. 1998). Fecal T was extracted from the samples in the Laboratory of Reproductive Ecology (P.L. Whitten, Director) and analyzed by radioimmunoassay for fT using techniques previously validated for this species (Brockman et al. 1995). Fecal T validation procedures yielded intra- and inter-assay coefficients of variation of 3.4% and 4.6%, respectively (Brockman et al. 1998). Previous studies showed that weekly mean serum T levels are well correlated with weekly mean fT concentrations (*r*=0.80–0.90; Brockman et al. 1998).

For comparisons of alpha and subordinate males, steroid concentrations of alpha males were compared to those of their own subordinates and analyzed using matched paired *t*-tests. Rank-related differences in fT concentrations were negligible among subordinates (mean±SE beta male T: 25.87±9.9 ng/g, gamma male T: 19.87±6.0 ng/g, *P*=0.44). Therefore, fT values were averaged for subordinates in groups with >1 subordinate male (which represented 33% of the groups). Hormone-behavior relationships in intensively sampled groups were assessed using Spearman rank order correlations between fT levels and frequencies of behavior (Brockman et al. 1998).

## Results

### Seasonal effects

Mean weekly fT levels differed significantly between the mating and birth seasons and between months. Mating-season adult males exhibited fourfold fT elevations over those in the birth season (mating season mean±SE: 262.20±61.6 ng/g, *n*=7 males; birth season: 62.92±16.02 ng/g, *n*=38 males; Mann-Whitney rank sum test: *T*=483.00, *P*≤0.001). During the birth season, mean fT levels of adult males sampled in August (121.12±45.2 ng/g) were threefold higher than those of males sampled in July (41.14±8.4 ng/g).

### Residence and transfer effects

Immigrant males did not have significantly higher mean weekly fT levels than resident males [resident males: 40.37±9.58 (SE) ng/g, *n*=19); immigrant males: 71.0±34.93 ng/g, *n*=12 males]. However, that may have been because most of the immigrants were sampled several weeks after their transfer. fT concentrations in immigrant males varied significantly with the number of days since transfer (one-way ANOVA: *F*=6.01, *P*=0.003, *n*=12 males). Males transferring into new groups during the previous 5 days had significantly elevated average fT concentrations over those transferring during the previous 15–30 and 60 days (mean 5-day fT: 188.47±85.8 ng/g, *n*=3; mean 30-day fT: 41.41±9.2 ng/g, *n*=5; mean 60-day fT: 28.89±6.3 ng/g, *n*=4). Moreover, peripheralized males, males who had been displaced or forcibly evicted from their groups, exhibited significantly lower weekly mean levels of fT than did those of resident, immigrant, and visiting males combined (7.55±10.83 ng/g, *n*=4 males; *P*=0.02). Their fT concentrations were indistinguishable from those of immatures during the birth season (4.43±1.7 ng/g, *n*=3).

### Rank and group stability effects

Mean weekly rates of aggression in the birth season varied significantly by rank. Alpha males initiated intermale aggression significantly more often did than subordinate males (weekly mean±SE alpha male aggression: 0.27±0.06, *n*=8 males; weekly mean subordinate aggression 0.08±0.04, *n*=12 males; *P*=0.009). Beta-ranked males exhibited significantly higher weekly mean rates of aggressive behavior than gamma-ranked males (beta weekly mean aggression: 0.123±0.1, *n*=4 males; gamma weekly mean aggression: 0.000, *n*=4 males; *P*=0.029). Alpha males (and females) were the sole recipients of submissive gestures (e.g., fear-grimaces/chatters, displacements) from other males. Similar rank-related differences were observed in fT concentrations, with fivefold higher levels in alpha males (Table 2). These analyses were done by averaging the 7- to 10-day fT values obtained for each male, with *n*=numbers of males.

Concordant with expectations, group instability was associated with significantly elevated weekly mean fT concentrations, particularly in groups containing multiple ranked males. Alpha males in unstable groups had nearly threefold higher fT levels than alpha males in stable groups (Table 2). fT levels in subordinate males, on the other hand, were remarkably similar across these divergent social conditions. Likewise, alpha males in unstable groups had higher fT values than their subordinate counterparts, a result that was not observed in stable groups. A two-way ANOVA showed a significant effect of rank (*F*=5.7, *P*=0.03) and stability (*F*=6.2, *P*=0.02) but no significant interaction between rank and stability effects (*F*=1.57, *P*=0.22).

### The presence of infants

Males in groups with infants did not have significantly higher fT (Table 2) or rates of aggression than males in groups without infants (aggression rates – infant group

**Table 2** Mean (±SE) rank-related fecal testosterone (ng/g)

| Males/groups | Alpha | Subordinate | Alpha–subordinate | Number of males | $P^a$ |
|---|---|---|---|---|---|
| All males[b] | 93.96±30.42 | 24.13±4.39 | 69.83 | 38 | 0.015 |
| Stable groups | 45.64±17.30 | 21.89±4.34 | 23.75 | 15 | 0.938 |
| Unstable groups | 122.79±38.59 | 26.80±4.16 | 95.99 | 23 | 0.008 |
| $P^c$ | <0.001 | 0.418 | | | |
| Infant groups | 61.64±15.80 | 26.45±6.07 | 35.19 | 14 | 0.175 |
| Non-infant groups | 124.78±43.22 | 25.83±4.24 | 98.85 | 14 | 0.109 |
| $P^c$ | 0.994 | 0.282 | | | |

[a] Paired *t*-test between alpha and subordinate
[b] In groups with observable rank relationships
[c] T-test between groups

**Table 3** Mean (±SE) fecal testosterone concentrations (ng/g) before, during, and after eviction (group name in parentheses; *n* number of fecal samples collected)

| Male | Before | *n* | During | *n* | After | *n* | *P* |
|---|---|---|---|---|---|---|---|
| Evicting males | | | | | | | |
| 282 (Tsyemelia) | 72.20±23.68 | 6 | 34.20 | 1 | 2.40 | 1 | |
| 9003 (Vaovao) | 41.70±15.90 | 2 | 279.60 | 1 | 14.70±10.97 | 3 | |
| 9006 (Vaovao) | 16.50 | 1 | 97.80 | 1 | 5.70±3.21 | 3 | |
| Mean | 60.57±17.12[a] | 9 | 137.20±73.53 | 3 | 9.09±4.77 | 7 | 0.010 |
| Evicted males | | | | | | | |
| 294 (Tsyemelia) | 9.40±4.03 | 8 | 2.70 | 1 | 0.03 | 1 | |
| 243 (Vaovao) | 5.65±1.25 | 2 | 7.30 | 1 | 4.55±0.73 | 4 | |
| Mean | 8.65±3.22 | 10 | 5.00±2.30 | 2 | 3.65±1.07 | 5 | 0.790 |

[a] *P*=0.008 vs mean fT in evicted males before eviction; Kruskal-Wallis one-way ANOVA on ranks

mean±SE: 0.11±/h, *n*=4; non-infant group mean: 0.15± 0.04 /h, *n*=5, *P*=0.86). That stable groups contained more infants than unstable groups suggests a confounding interaction between infant and stability effects. A two-way ANOVA showed, however, no significant effect of infant (*F*=1.02, *P*=0.35), stability (*F*=4.3, *P*=0.06) or their interaction (*F*=0.31, *P*=0.59).

Although there appeared to be no overall tendency for T elevation in the presence of infants, alpha males residing in unstable groups had elevated fT levels prior to birth (Andafy) and prior to the aggressive incursions of neighboring groups (Celeste). Observations surrounding parturition in Andafy female 191 suggest that birth may precipitate elevations in fT in some circumstances. A recent immigrant, male 160 approached and sat next to a new infant without aggression from either the mother or alpha male 203, the likely father. However, Fig. 1 shows a marked elevation in male 203's fT levels the day before parturition and elevations in fT in both males 3 days before the infant's birth, associated with increased tension and inter-male conflict. Alpha male 203's fT levels were almost twice those of subordinate male 160 before birth and fell after parturition. Further suggestive evidence that males facultatively elevate fT in the presence of newborns includes hormonal data from the opportunistically sampled Kashka group containing a 2-day-old infant. The subordinate male in this group (9025) exhibited a twofold elevation in fT concentrations associated with aggressively blocking the immigration attempts of neighboring Rengor male 9 (see below).

### Aggression and alterations in group structure

Weekly mean rates of aggression varied substantially among males. Males evicting residents and those transferring or attempting to transfer exhibited almost twice [0.034±0.01 (SE)/h, *n*=5] the average rate of aggression (0.018±0.01/h, *n*=18) than those who do not transfer or evict residents, while others showed no aggression (*n*=5). Serial fecal samples obtained from three evicting

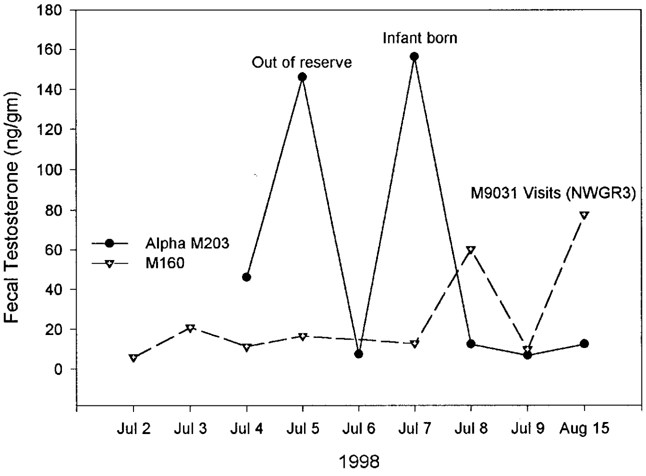

**Fig. 1** Profile of daily fT concentrations in Andafy's alpha male 203 and subordinate male 160 associated with the birth of an infant

and two evicted focal males before, during, and after eviction showed that average fT concentrations varied significantly among evicting males, who exhibited substantially higher fT levels before and during eviction than after (before: 60.6±17.1 ng/g; during: 137.20±73.5 ng/g; after: 9.09±4.8 ng/g; *P*=0.01; Table 3). Moreover, fT concentrations in evicting males prior to expulsion were significantly elevated over those of evicted males.

Males observed transferring (*n*=3) and attempting to transfer (*n*=1) varied in their rates of aggression depending upon transfer success and rank. Subordinate male 9 who attempted, but failed, to transfer exhibited significantly higher rates of aggression than males successfully transferring into new groups (mean attempted transfer aggression: 0.07±0.1 /h, *n*=1 male; mean transfer aggression: 0.013±0.01 /h, *n*=3 males; *P*=0.034). The single gamma-ranked male who successfully transferred into a new group did so without aggression, retaining his third-rank position in the new group. Concordant with expectations, fT concentrations in adult males who were aggressive during transfer/attempted transfer were significantly elevated above those who did not engage in aggression during immigration (mean aggression-related fT: 204.61±94.0 ng/g, *n*=3 males; mean non-aggression-related fT: 22.83±19.2 ng/g, *n*=1 male; *P*=0.024). Rank effects of aggression-related fT concentrations in transferring males were negligible (mean weekly fT of aggressive alpha males: 223.33±112.6 ng/g, range 1,458.6, *n*=2 males; mean weekly fT of aggressive subordinate males: 40.22±13.7 ng/g, range 190.0, *n*=2 males; Mann-Whitney rank sum test: *T*=179, *P*=0.18).

The only adult male to aggressively attempt to transfer, male 9 (13 years) was Rengor's second-ranked male, and had transferred six times in the previous 13 years. Male 9 tried repeatedly to transfer into several of the neighboring groups but encountered high levels of aggression from their resident males. He exhibited an almost threefold higher rate of aggression during his transfer attempt into Kashka [0.08±0.1 (SE)/h] than during his prior immigration attempts (0.03±0.03 /h, *P*=0.41), this last attempt targeting a group containing an infant. Male 9's hormone profile (Fig. 2) shows marked increases in fT coincident with each of three transfer attempts, with substantially higher fT levels during the last immigration attempt (96.6 ng/g) than in previous attempts (17.6±6.8 ng/g; not shown).

Group members varied in their response to male visits and immigration attempts. A higher proportion of subadult and younger adult males (64%) than older males (36%) entered neighboring groups and approached within 1 m of newborns without eliciting aggressive responses from residents. fT levels did not differ significantly (*P*=0.35) in the adult [83.6±39.9 (SE) ng/g, *n*=6 males] and subadult (19.8±10.6 ng/g, *n*=4 males) male visitors for whom samples were available. It is interesting to note, however, that while subadults received more positive *behavioral responses*, they elicited *hormonal responses* from resident males that suggested that these visits were not entirely benign. Figure 3 shows the fT responses of Tsyemelia males to visits by males 9093 (3 years) and 9096 (5 years). Alpha male 282 exhibited marked elevations in fT in conjunction with both visits, whereas beta male 92 showed a more muted response to the second visit. Moreover, gamma-ranked male 294 (8 years) exhibited a decline in fT throughout this period and was forcibly evicted after the second visit, suggesting that even brief "benign" visits can substantially alter group structure.

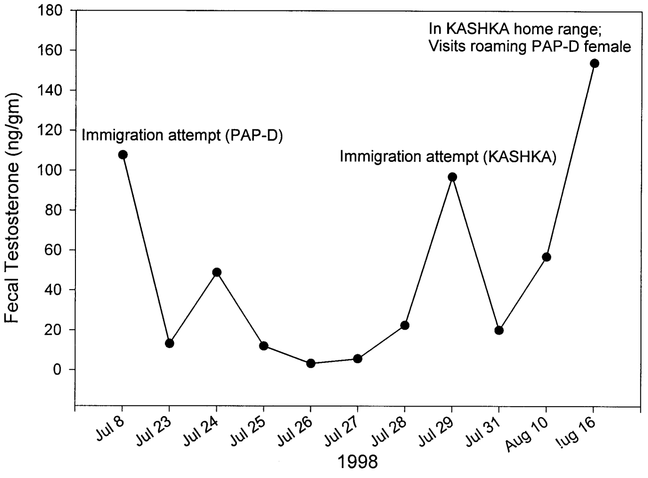

**Fig. 2** Profile of daily fT concentrations in Rengor's male 9 associated with his attempts to immigrate into the Pap-D and Kashka groups

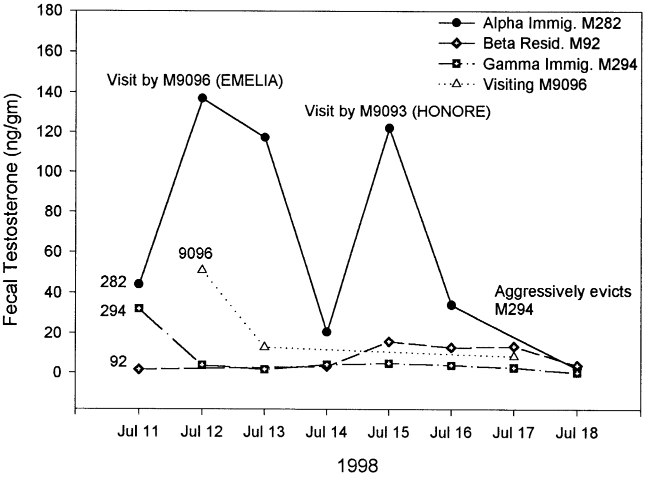

**Fig. 3** Profile of daily fT concentrations in Tsyemelia's resident male 92 and immigrant males 282 and 294 associated with eviction of male 294 and visits by Emelia's male 9096

Group structure was also altered by internal events associated with aggression and rank reversal. Vaovao's alpha male 243 was evicted in an attack by Vaovao residents (Fig. 4) and relegated thereafter to peripheral status, a position enforced by the new alpha male 9003. Figure 4 shows the hormonal indicators of impending attack and subsequent rank reversal. Male 9003's fT levels increased substantially just after acquisition of alpha rank while those of the evicted male 243 remained low throughout the 10-day sampling period.

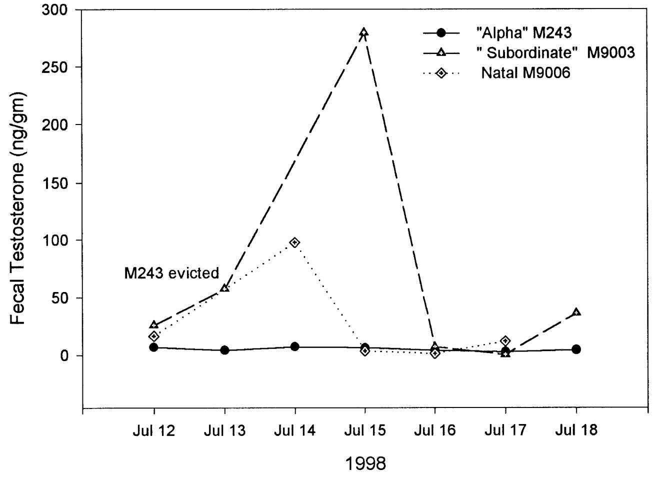

**Fig. 4** Profile of daily fT concentrations in Vaovao's "alpha" male 243 and "subordinate" males 9003 and 9006 before and after the eviction of male 243

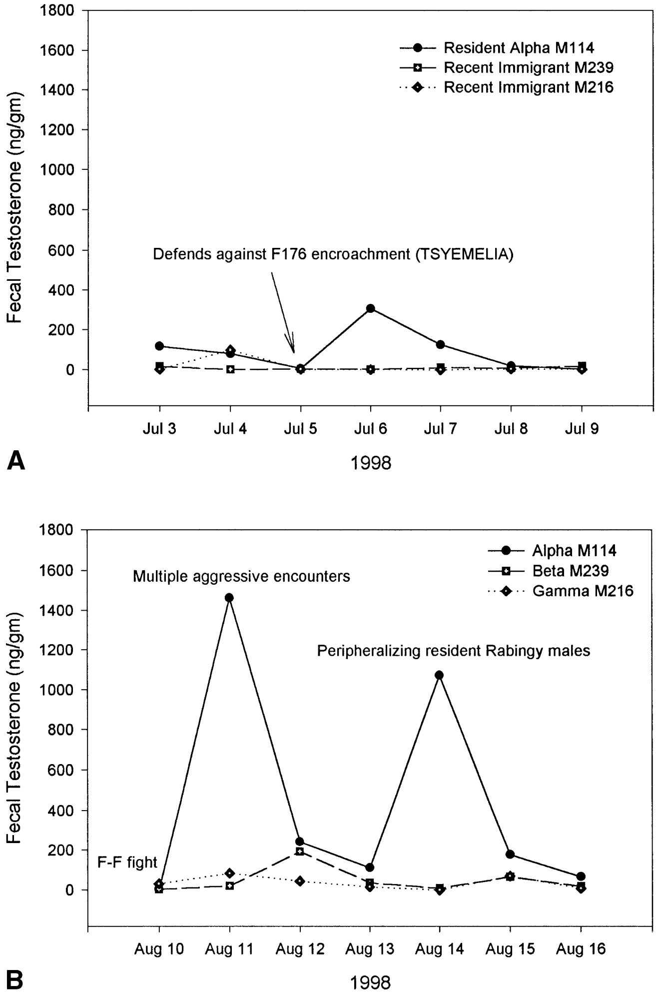

**Fig. 5** Profile of daily fT concentrations in Pap-D's resident male 114 and immigrant males 239 and 216 before (**A**) and after (**B**) the resident female's boundary dispute with the neighboring Rabingy female and the latter's recruitment of Pap-D males

Finally, group structure was substantially altered through the actions of females rather than males. Over a 3-month period, Rabingy female 284 evicted and attempted to evict the Sarvad and Pap-D females from their home ranges, recruiting several of their adult males. In the second instance, a series of aggressive encounters and chases between the females ensued, resulting in considerable fluidity in the spatial relations and interactions of Pap-D males. Figure 5A shows the T profiles of the Pap-D males 1 month prior to female-female aggression, demonstrating that alpha male 114 had substantially higher T levels than the beta- and gamma-ranked males. Figure 5B shows the significant elevations in fT that occurred in male 114 during these female boundary disputes, levels that were sixfold higher than his previous levels (not shown) and well within the range observed in adult males during the breeding season (Brockman et al. 1998).

## Discussion

### Temporal patterning of T excretion

The hormone-behavior interactions described here and in our previous research (Brockman 1994; Brockman and Whitten 1996; Brockman et al. 1998) underscore the broadly seasonal nature of reproductive function in sifaka at BMSR. Adult males experienced a 74% decline in mean weekly fT concentrations from the mating to the birth season, consistent with the ecologically mediated testicular cyclicity observed in other seasonally breeding mammals (reviewed in Lincoln 1981), including strepsirrhines (*Microcebus murinus*: Petter-Rousseaux and Picon 1981; *Hapalemur aureus*: Glander at al. 1992; *Lemur* spp.: Evans and Goy 1968; Bogart et al. 1977; *P. verreauxi*: Kraus et al. 1999). Hormonal result data concur with morphometric data showing that mean birth season testes volumes regress to 81.4% of the average seasonal maximum (D.K. Brockman and A.F. Richard, unpublished data) and suggest that males exhibit a less extreme degree of testicular seasonality than indicated by the 3-month mating season (Richard 1974; Brockman and Whitten 1996). These results, however, obscure important events at the phenotypic level, where social environment and life history events exert their influence most directly on male fitness. Hormone data suggest that, under certain circumstances, individual differences in fT extend beyond the mating season. Variation in androgen responsiveness among males was associated with varying dispersal tactics and associated aggression, suggesting that sociodemographic factors may override ecological constraints on seasonal testicular function in individual males during the birth season. The fitness benefits of aggression-related fT elevations during the birth season are unknown, but one might postulate that, as in ringtailed lemurs (Pereira and Weiss 1991), successful birth season aggression may improve a male's chances of being favored as a mate in the following mating season.

## Transfer

The finding that fT concentrations of recent immigrants were only slightly elevated above those of residents was unexpected, but most likely reflects a sampling-related temporal disjunction between actual immigration and subsequent residence-based androgen levels.

Evidence that fT variations may more accurately reflect temporal events and male sensitivity to particular events derives from androgen-behavior interactions among the Pap-D males during their transfer into the Rabingy group. During immigration, mean fT levels in these males were eightfold higher than pre-transfer levels (range: three- to tenfold higher). Alpha male 114 exhibited the most marked increase in fT concentrations, those occurring during and after immigration being more than twice the average observed in older adult males during the breeding season (e.g., 330 ng/g; Brockman et al. 1998).

The roles played by ecological and/or social factors in male transfer decisions are not known, but hormonal data obtained from seven females showed that males could not have accrued immediate reproductive benefits from transferring during the birth season. Fecal estradiol levels in focal females averaged 1.10± 0.55 (SE) ng/g, being 10- to 50-fold lower than those observed in estrous females during the breeding season (Brockman and Whitten 1996). Continuous monitoring of male transfers between July 1993 and January 1995 (K.S. Kubzdela, unpublished data) indicate that there may be seasonal effects on male transfer success, males experiencing higher success rates during the non-mating than the mating season (non-mating season transfer frequency: 3.0/month, *n*=23 males; mating season transfer frequency: 2.67/month, *n*=8 males).

## Rank effects on T excretion

Social rank had a profound influence on fT variations among males. Alpha males excreted significantly higher fT levels than subordinate males, similar to the mating season patterning of fT excretion (Brockman et al. 1998), confirming previous findings reported by Kraus et al. (1999). Thus, it appears that alpha males maintained moderately elevated fT levels even during the birth season when inter-group aggression waned (Richard and Heimbuch 1975), indicating that there may be social advantages to maintaining high rank and elevated androgen levels year-round. One such advantage may be the ability of alpha males to be more physiologically responsive than subordinate males to external challenges that threaten group cohesion. For example, fT was more responsive to group instability in high-ranking males than in subordinates. In this regard, high-ranking males residing in unstable groups maintained significantly higher levels of fT than those living in stable groups, a trend that persisted between alpha and subordinate males within unstable groups. Among catarrhines (reviewed in Whitten 2000), T exhibits a consistent relationship with rank only during periods of rank instability in some taxa (*Papio anubis*: Sapolsky 1982, 1986), but has a more persistent relationship to rank in species (e.g., mandrills: Wickings and Dixson 1992; guenons: Eberhardt et al. 1980; Steklis et al. 1985) with a well-differentiated alpha male (Whitten et al. 1998; Whitten 2000). Androgen-rank interactions in sifaka appeared to resemble both of these patterns, since the significantly elevated fT concentrations observed in alpha males were amplified during periods of group instability, in association with eviction and aggressive transfer.

## Effects of infants on T excretion

Data from birds suggest that polygnous species are less hormonally responsive to social cues than monogamous species during the mating season (Wingfield et al. 1990), but this appears not be to the case in some carnivores which exhibit substantial parental care (dwarf mongooses: Creel et al. 1993). Sifaka are polygamous and males exhibit no direct parental care (Brockman 1994). Thus the “challenge hypothesis” (Wingfield et al. 1990) would predict that male sifaka residing in groups containing infants would have substantially lower fT concentrations than those living in groups without infants and, indeed, this appears to be the case, although further data will are needed to confirm this result. The reasons for this are unknown, but males residing in stable groups may have been enhancing their reproductive success by avoiding the negative fitness consequences of social disruption and/or ensuring infant survival by remaining in their groups after parturition and defending against male immigration attempts. However, contrary to the “challenge hypothesis” males in two social groups (Andafy, Kashka) appeared to elevate fT concentrations facultatively in anticipation of birth and while defending against the aggressive challenges of transferring males in the presence of newborns, suggesting that some males may be particularly responsive to parturition events and the risk of male infanticide. Rengor male 9’s aggressive transfer attempt was successfully repulsed by Kashka males, introducing the possibility that, like protector males in other species (van Schaik 2000), sifaka, and particularly putative fathers, may employ effective counterstrategies to the immigration attempts of older males, thereby reducing the risk of male infanticide. Our studies of counterstrategies to infanticide risk in sifaka at BMSR continue, but it may very well be that the very low frequency of infanticide at this site (Richard et al., unpublished data) is in large measure due to the effectiveness of these male counterstrategies.

The overall diminished fT levels in males residing in those groups containing infants, however, remains to be explained. In the absence of external challenges, the costs of maintaining high androgen levels in anticipation of aggression could be substantial for males, including, perhaps reduced survivorship (Dufty 1989), suppression of the immune system, and infertility (Hillgarth et al. 1997), although we have no direct evidence for this in sifaka. Nevertheless, the coincidental relationship observed between substantially elevated fT concentrations in alpha males residing in unstable groups, high levels of aggression in particular alpha males, and the low numbers of births in these groups suggests a potential fitness cost to maintaining high androgen levels beyond the mating season.

### The effects of group stability and aggression on T excretion

In accordance with our mating season findings (Brockman et al. 1998) and previous studies of macaques and baboons (*Macaca fuscata*: Eaton and Resko 1974; *Macaca mulatta*: Gordon et al. 1976; *P. anubis*: Sapolsky 1982, 1986), birth season fT levels in alpha males residing in unstable groups were significantly elevated over those living in stable groups. Social disruption may have substantial costs for males, particularly alpha males, including increased aggression, injury, and eviction. This androgen-rank effect of destabilization is not unexpected. High rank affords sifaka males priority of access to estrous females (Brockman et al. 1998; Brockman 1999) so that any challenge to male rank via group destabilization could profoundly affect a male's within-group mating success in the following mating season. Significant aggression-related fT elevations have also been observed in semi-free-ranging *Lemur catta* males during the unstable mating season (Cavigelli and Pereira 2000), indicating a role of fT in mate competition. Fecal cortisol (fC) data (Brockman and Whitten 1999; unpublished data) suggest that the adrenal cortex may contribute to androgen elevations in sifaka during social disruption. Alpha males residing in unstable groups have significantly higher fC levels than their subordinates, and among subordinate males, those residing in unstable groups had significantly higher fC concentrations than those residing in stable groups (Brockman et al. 1999). Similar rank-related C effects have been observed in wild *P. anubis* associated with particular behavioral styles (Sapolsky 1989).

Rates of aggression and fT concentrations were significantly increased in males observed evicting residents and in those attempting to aggressively transfer into new groups. Future studies will assess the degree to which evicting males elevate their fT levels in anticipation of combat and forcible ejection and whether or not hormonal responses precede behavioral responses as our preliminary data suggest. If confirmed, these results may provide new insights into the causal relationship of androgen-behavior interactions in sifaka.

In conclusion, these preliminary data are the first to show that fT reflects specific events as well as social states in free-ranging sifaka. Contrary to the patterning of serum T observed in other mammals (baboons: Alberts et al. 1992; badgers: Woodroffe et al. 1995), variation in fT concentration did not exhibit any simple general relationship to residence status, the presence of infants, or the risk of male infanticide in sifaka. The hormone-behavior relationship observed in *P. verreauxi* at BMSR was much more nuanced, reflecting phenotypic differences and social events. In general (i.e., in stable groups), fT was lower in the birth season, but during periods of group instability, fT concentrations increased markedly whatever the season. Birth season elevations in fT were a consequence of social disruption resulting from male movements between groups and the particular responses of individual males to dispersal events. The hormonal data, in particular, provide a provocative new approach for exploring potential mechanisms underlying demographic destabilization influences within groups.

Our continued studies will elucidate the degree to which hormonal responses in sifaka may precede behavioral responses and occasionally register reactions not evident in the behavioral response, being perhaps predictive of future events. That these reactions occurred primarily in alpha males suggests that resident males differ in their assessment of destabilizing influences, most likely due to different social opportunities. These findings are important for the new insights they provide into the role of androgens in mediating male dispersal, life history, and reproductive strategies, and show that investigations of androgen-behavior interactions in free-ranging populations can be a powerful new tool for assessing the contextual and motivational basis of social behavior.

**Acknowledgements** The authors are grateful to the government of Madagascar and ANGAP for granting us permission to conduct research at Beza Mahafaly Special Reserve (BMSR). We especially thank Dr. Joel Ratsirarson, ESSA, Departement des Eaux et Forets, Universite D'Antananrivo, and his extremely talented staff at BMSR for their expertise in helping us census the sifaka population and for the many hours of warm and lively dinner conversations. Sylvia, Rigobert, Elahavelo, and Edidy provided invaluable assistance in locating and surveying the sifaka social groups in the reserve and Lanto's supervision of the camp staff made the return home from the forest at the end of the day a sheer joy. This research would not have been as successful as it was without the intelligence, dedication, and enthusiasm of graduate students Becca Lewis and Heather Patisaul. Their eagerness to work and skill with which they accomplished the task established a new standard for field assistants that will be difficult to match. We thank Kashka Kubzdela for allowing us to include her unpublished data on male transfers. The manuscript was substantially improved by comments provided by Susan Alberts, Michael Pereira, Karen Strier and three anonymous reviewers, for which we are extremely grateful. Finally, this research would not have been possible without the generous support provided to D.K.B. from the Arts and Sciences Research Council at Duke University and The Margot Marsh Biodiversity Foundation, and to P.L.W. from Emory University. D.K.B. especially thanks Margot Marsh for her many years of friendship, encouragement, and for sharing her passionate concern for primates the world over. The research reported here complies with the current laws of the country in which it was conducted.

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