**Endocrine Correlates of Reproductive Status in Breeding and Nonbreeding Wild Female Moustached Tamarins**

Petra Löttker1,2,5, Maren Huck1,3, EckhardW. Heymann1 and Michael Heistermann4

1 Abteilung Soziobiologie, Deutsches Primatenzentrum, Kellnerweg 4, 37077 Göttingen, Germany.

2 Institut für Neuro- und Verhaltensbiologie, Abteilung Verhaltensbiologie, Westfälische Wilhelms-Universität Münster, Germany.

3Lehrstuhl für Verhaltensforschung, Universität Bielefeld, Germany.

4 Abteilung Reproduktionsbiologie, Deutsches Primatenzentrum Göttingen, Germany.

5To whom correspondence should be addressed; e-mail: ploettker@dpz.gwdg.de

In callitrichid primates, reproduction is usually restricted to a single female per group. Reproductive rate is high and the occurrence of a postpartum estrus can lead to simultaneous lactation and pregnancy. In contrast, nonreproductive females often show ovarian inactivity. However, most studies on callitrichid reproductive physiology have been conducted in captivity, where conditions differ considerably from those in the wild, so that reproductive conditions may be strongly modified. Using fecal estrogen and progestogen measurements to monitor female reproductive status in 2 groups of wild moustached tamarins (*Saguinus mystax*), we examined 1) whether reproductive females in free-ranging groups also show postpartum estrus and 2) whether nonreproductive females demonstrate signs of ovarian activity. In both reproductive females, clear changes in the excretion pattern of progestogen and estrogen metabolites over time in combination with information on parturition dates allowed us to differentiate between pregnancy, a period of postpartum ovarian inactivity lasting for 54 and 64–82 days, and a period of ovarian activity before conception. Nonreproductive females demonstrated temporal fluctuations in hormone concentrations and absolute hormone levels that were similar to ones in the breeding females during the phase of ovarian activity. The results suggest that, in contrast to most captive female tamarins, reproductive females in wild groups of moustached tamarins do not have a postpartum estrus and that nonreproductive females show ovarian activity despite the presence of a breeding female. We therefore conclude that findings from captivity should be only carefully compared to the situation in the wild.

**KEY WORDS:** moustached tamarin; *Saguinus mystax*; fecal steroids; post-partum estrus; reproductive monopolization.

**INTRODUCTION** Callitrichids are characterized by a unique combination of traits that distinguish them from other primates and most other mammalian species. Generally, they live in small groups of one to several adult males and females that may contain both related and unrelated individuals (Huck *et al.*, submitted; Nievergelt *et al.*, 2000). Regardless of the number of adult females in a group, reproduction is usually restricted to a single female, which gives birth to heavy and rapidly developing twins (Garber and Leigh, 1997). Infants are raised cooperatively with the help of all group members, and particularly males invest intensively in infant-carrying (Garber, 1997; Goldizen, 1988; Savage *et al.*, 1996b), which imposes high energetic costs (Achenbach and Snowdon, 2002; S´anchez *et al.*, 1999). Given that in captivity callitrichid females exhibit a postpartum estrus, usually ·2–4 weeks after birth (French *et al.*, 2002, for review), pregnancy, lactation and infant-carrying can occur simultaneously. The energetic burden posed by these unusual characteristics in the reproductive biology of callitrichids plays a key role in discussions about the evolution of polyandrous mating systems and alloparental care (Caine, 1993; Eisenberg, 1977; Goldizen, 1990; Tardif *et al.*, 1993). In callitrichids, helpers are essential to rear the young (Goldizen, 1987), and females compete for breeding-opportunities and (especially male) helpers (Garber, 1997). The proximate mechanisms underlying inter-female competition and ensuing reproductive monopoly of a single breeding female appear to be species-specific and include both behavioral and physiological factors (Abbott *et al.*, 1993; French, 1997). In particular, high inter-female aggressiveness (French and Inglett, 1989; Inglett *et al.*, 1989), prevention of ovarian cyclicity and/or conception in nonbreeding females (Abbott, 1991), and infanticide on offspring of secondary breeding females (Digby, 1995) can occur. Almost all information concerning callitrichid reproductive physiology, stems from studies of captives, wherein conditions may differ considerably versus the situation in the wild, so that reproductive conditions may be strongly modified. First, captives are usually housed in pairs or extended family groups with their (adult) offspring, while wild groups may also contain unrelated adults. In contrast to non-related group members, reproductive (in)activity of offspring might be mainly shaped by mechanisms of inbreeding-avoidance and could partly be understood in terms of inclusive fitness gains. Secondly, in captivity nonreproductive females are forced to maintain closer contact with the reproductive individuals due to limitation of space. This might facilitate agonistic interactions and the effectiveness of olfactory cues, which may mediate reproductive failure in nonbreeding females (Epple and Katz, 1984). Thirdly, energetic constraints are less severe or absent in captivity, so that postpartum estrus and a higher reproductive rate are energetically feasible. These assumptions seem to be supported by a study of Savage *et al*. (1997), who found that wild female cotton-top tamarins (*Saguinus oedipus*) experienced postpartum reproductive inactivity that averaged *ca.* 144 days and that daughters appeared to exhibit ovarian cycles. Similarly, Albuquerque *et al*. (2001) and French *et al*. (2003) found evidence for ovarian cyclicity in nonreproductive female common marmosets (*Callithrix jacchus*) and golden lion tamarins (*Leontopithecus rosalia*) in wild groups. In order to better understand the evolution of callitrichid reproductive strategies and mating systems, it is important to test whether the findings reported by Savage *et al*., Albuquerque *et al*., and French *et al*. also apply to other species of marmosets and tamarins. Moustached tamarins (*Saguinus mystax*) are of particular interest because they seem to exhibit a higher degree of polyandry in comparison to other callitrichid species (Löttker *et al*., unpublished data). In the wild, groups comprise 1–4 adult males and 1–4 adult females (Soini and Soini, 1990). Yet the adult sex ratio is biased in favor of males, and with 6.8% of groups containing a fourth male the mean number of males in moustached tamarin groups is higher than in most other callitrichid species (Heymann, 2000). Further, in previous studies on moustached tamarins, groups consistently contained only one breeding female (Garber *et al.*, 1984; Heymann, 1996), and in the rare cases in which simultaneous pregnancies of 2 group females occurred, only the offspring of one female survived (Garber *et al.*, 1993; Ramirez, 1989; Smith *et al.*, 2001). Breeding females mate polyandrously with several or all adult group males (pers. observ.), thus providing a high potential for sperm competition. Male moustached tamarins have got the largest relative testes size among callitrichids (Heymann, 2000). Like other callitrichids, female moustached tamarins show no externally obvious sign of ovulation (Dixson, 1983; contra Sicchar and Heymann, 1992), and data on cycle and gestation length from captivity are missing for the species. Against this background our overall aim was to provide information on the reproductive endocrinology of wild female moustached tamarins, via behavioral observations and noninvasive endocrine monitoring of reproductive status. Our specific objectives were to examine whether 1) reproductive females show a postpartum estrus shortly after parturition, and 2) whether nonreproductive females show signs of ovarian endocrine activity.

**METHODS**

**Study Site, Study Groups, and Group Follows** The study site is the Estación Biológica Quebrada Blanco (EBQB) in the Amazon lowlands of northeastern Peru´ (4±21’S 73±09’W; Heymann, 1995). The data are from 2 well-habituated groups (W and E) of moustached tamarins (*Saguinus mystax*) with individually known group members. Both groups are under regular observation since May 1999 (W) and January 2000 (E). From January to December 2001 we performed all-day follows of both groups, usually 7 days per week. We observed groups from leaving the sleeping tree in the morning until entering the next sleeping tree in the afternoon (average daily observation time: 9.2 h), yielding a total of 3004h on 330 days for W and 3257h on 351 days for E. The continuous group follows were possible via simultaneous observations of the 2 groups by Löttker and Huck with the help of 4 field assistants. Throughout the major part of the study period, W comprised 7 monkeys including one reproductively active female (WF1) and 3 adult males (Table I). WF1 showed clear signs of pregnancy—rounded abdomen and enlarged nipples—by the beginning of November 2001, but she died on December 3, 2001, *ca.* 2 weeks before the estimated parturition date and 1 month before the end of the study, probably due to an injury. Following her death, the group split: 2 males emigrated and the juvenile male disappeared (Lo¨ ttker *et al*., unpublished data). E comprised 9 monkeys, including 1 reproductively active female (EF1), 2 nonreproductive adult females (EF2, EF3), 1 female infant/juvenile (EF4), and 3 adult males (Table I). EF2 and EF3 were both daughters of EF1 and EM3 (Huck *et al.*, submitted), and at the onset of the study, they were¸31mo old (Table I).We saw neither female mate with a group male and they showed no sign of pregnancy. They disappeared (presumably emigrated) together on September 16, 2001, 3.5 mo before the end of the study (Löttker *et al*., unpublished data).

**Sample Collection and Hormone Analysis**

We collected fecal samples from the 4 adult females throughout the entire study period whenever an unambiguously identified individual defecated. In addition, we occasionally collected samples from the juvenile female, EF4. Due to their arboreal life—they mainly stay 9–16 m high in the trees (Heymann and Buchanan-Smith, 2000)—and feeding ecology— moustached tamarins are mainly frugivorous and almost always swallow seeds (Knogge and Heymann, 2003), so that many samples consisted of pure seeds without any fecal matter—sample collection was difficult (see also Cordeiro de Sousa *et al*., 2002). On average we obtained 2 fecal samples per female per week (range 0–7 samples; Table II), and gaps between samples of the same individual were ·24 days. We attempted to collect samples at roughly the same time of day, but this was impossible and samples had to be collected opportunistically during the whole day (earliest sample: 06:11h; latest sample: 16:35h; in total *ca.* 30% of samples collected in the first half (*<*11:00h) and *ca.* 70% in the second half (*>*11:00h) of the activity period). On 7 occasions, we collected a morning and afternoon sample from the same individual. Because progestogen and estrogen concentrations are significantly higher in the morning samples (Wilcoxon matched paired test, both hormones: *Z* D 2*:*37; *p* D 0*:*018), we exclusively generated hormone profiles from afternoon samples. Immediately after collection we put the whole sample in a polypropylene tube and completely covered it with 3 ml of 96% ethanol (Wasser *et al.*, 1988). We labeled the tube with sample number, monkey identity, and date and time of collection, and sealed it with Parafilm. We stored samples at ambient temperatures in the field for 21 days on average, after which we brought them to Iquitos and placed them in a refrigerator (4±C) until shipment to the laboratory for hormone analysis. We extracted hormones in the original ethanolic solvent per Kraus *et al*. (1999). In brief, we homogenized samples via a metal spatula, and vortexed the fecal suspensions for 15 min. Following centrifugation at 3000 rpm for 10 min, we decanted the supernatants into glass tubes and stored them at 4±C. Then we re-extracted fecal pellets with 3 ml absolute methanol. Before the second centrifugation, we removed seeds *>*5 mm (Curtis *et al.*, 2000). We combined supernatants of both extractions, recorded the total volume, and stored part of the extract at ¡20±C until hormone analysis. We dried the remaining fecal pellets in a vacuum oven at 50±C, and determined the dry mass of individual samples. For hormone analysis, we used only extracts from samples with a minimum dry mass of 0.02 g. The efficiency of the extraction procedure, determined in a subset of samples (*n* D 40) by monitoring the recovery of 3H-progesterone (3H-P4, »30000 cpm), added to the samples prior to homogenization, is 90.0 § 9.0% (mean § SD). We measured fecal extracts for immunoreactive progestogen and estrogen metabolites via enzyme immunoassay. Because breeding female moustached tamarins were not available in European zoos or other institutions in Europe, it was not possible to conduct a radiometabolism study to determine the major progesterone and estrogen metabolites or to collect matched blood and fecal samples for a biological validation of our fecal hormone measurements. Consequently we measured fecal extracts for concentrations of immunoreactive pregnanediol-3-glucuronide (PdG) and total estrogens (Et). Both groups of hormones represent quantitatively abundant fecal metabolites of progesterone and estradiol, respectively, in mammals (Heistermann *et al.*, 1995), and their measurement in feces accurately reflects female reproductive function in several primate species (Heistermann *et al.*, 1996; Ostner and Heistermann, 2003; Shideler *et al.*, 1993; Ziegler *et al.*, 2000), including callitrichid species (French *et al*., 2003; Heistermann *et al.*, 1993; Savage *et al.*, 1997; Ziegler *et al.*, 1996). Furthermore, application of 2 other progestogen assays—specific progesterone assay and group-specific assay for 5*®*-reduced- 20-oxo-pregnanes—to the fecal extracts revealed similar profiles and highly significant correlations between the different progestogen measurements in both breeding females (Spearman Rank Order Correlations: *r* D 0*:*67–0.93, *p <*0.0001–0.001; data not shown). Thus, we are highly confident that our endocrine measurements provide reliable information on reproductive status in our subjects. We measured immunoreactive PdG per Heistermann *et al*. (1993) with the exception that we used PdG instead of pregnanediol as standard. We diluted fecal extracts 1:5 to 1:1500, depending on reproductive status, in assay buffer (0.04MPBS, pH 7.2) and took duplicate 50 *¹*l aliquots to assay along with 50 *¹*l aliquots of reference standard in doubling dilutions over the range of 6.25–1600 pg/well. Sensitivity of the assay at 90% binding was 12 pg. Serial dilutions of fecal extracts from different reproductive stages— early and late pregnancy, non-pregnant status—yielded displacement curves parallel to that obtained with the PdG standard. Intra-assay and interassay coefficients of variation assessed by replicate determination of high- and low value quality controls are 3.8% (*n* D 16) and 7.7% (*n* D 33) (high), and 6.4% (*n* D 15) and 13.3% (*n* D 33) (low), respectively. We measured immunoreactive total estrogens (Et) per Ostner and Heistermann (2003). We diluted fecal extracts 1:5 to 1:3200, depending on reproductive status, in assay buffer (0.04 M PBS, pH 7.2) and took duplicate 50 *¹*l aliquots to assay along with 50 *¹*l aliquots of reference standard (estradiol-17*¯*; E2) in doubling dilutions over the range of 1.9–250 pg/well. Sensitivity of the assay at 90% binding was 1.5 pg. Serial dilutions of fecal extracts from different reproductive stages produced displacement curves parallel to the one obtained with theE2 standard. Intra- and interassay coefficients of variation, determined are 7.5% (*n* D 16) and 12.0% (*n* D 36) (high), and 5.4% (*n* D 16) and 14.2% (*n* D 36) (low), respectively. All hormone concentrations are *¹*g/g dry mass of feces (Wasser *et al.*, 1993).

**Interpretation of Fecal Hormone Profiles**

We used the patterns of fecal PdG and Et excretion to determine reproductive function in the individual females. According to Savage *et al*. (1997), simultaneous and regular elevations in progestogen and estrogen excretion over baseline indicate a period of ovarian activity, while consistently low baseline levels over extended periods of time (*>*30 days) represent a phase of ovarian inactivity. Accordingly, a sustained rise (¸3 successive samples covering a period of ¸10 days) in progestogen and estrogen levels above a defined threshold value (2 standard deviations above the mean of the preceding baseline values: Ziegler *et al.*, 2000) indicates the onset of ovarian activity when prior hormone levels indicated a phase of ovarian inactivity. Due to gaps in sample collection and therefore partially incomplete hormone profiles as well as an intraindividual day-to-day variability in hormone concentrations, both an assignment of individual ovarian cycles and determinations of cycle length and the exact time of conception were not possible. We further related hormone data to male mate-guarding: staying in spatial proximity with the female over ¸1 days (Andersson, 1994; Birkhead and Møller, 1998).

**RESULTS**

**Reproductive Females** In both groups, reproduction was restricted to one female, which gave birth to twin offspring at the beginning of the study in January (EF1) and February (WF1) 2001. Both females had been reproductively active in the previous year and EF1 also gave birth to offspring in January and December 2002 (C. Flores Amasifuén and M. Shahuano Tello, pers. comm.). The births toEF1andWF1between 2000 and 2002 revealed a median interbirth interval of *ca.* 334 days (Table III). Figure 1 shows the profiles of PdG and Et excretion throughout a complete annual reproductive cycle in relation to periods of male mate-guarding for each of the two breeding females. Overall, both females exhibited clear changes in the excretion pattern of progestogen and estrogen metabolites over time. At the onset of the study, both females were in their last 3 (EF1) to 6 weeks (WF1) of gestation. Following parturition, concentrations of both hormones, particularly estrogens, dropped markedly and remained consistently low for the next 54 (WF1) and 64–82 days (EF1; no exact value due to gap in sample collection), with no sign of cyclic ovarian function. In ¸90% of days on which hormone values are available, concentrations lay below 4 *¹*g/g (EF1) and 6 *¹*g/g (WF1) for PdG, and 0.15 *¹*g/g (EF1) and 0.2 *¹*g/g (WF1) for Et, and were thus comparable, particularly for Et, to the low concentrations in samples from the juvenile female EF4 (medians WF1: 3.4 *¹*g/g for PdG, 0.08 *¹*g/g for Et, *n* D 17; medians EF1: 1.6 *¹*g/g for PdG, 0.03 *¹*g/g for Et, *n* D 23; medians EF4: 0.2 *¹*g/g for PdG, 0.03 *¹*g/g for Et, *n* D 6). From April onwards, concentrations of PdG and Et clearly increased and subsequently fluctuated between periods of low and elevated levels, presumably indicating ovarian activity. Since gestation length in other tamarin species ranges from 150 to 184 days (*Saguinus fuscicollis* 150 days: Heistermann and Hodges, 1995; *S. bicolor* 160 days: Heistermann *et al.*, 1987; *S. oedipus* 184 days: Ziegler *et al.*, 1987a), we assumed the onset of pregnancy of our females to be in June/July (WF1) and July/August (EF1). Before that time, progestogen and estrogen levels exceeded 4 *¹*g/g (WF1) and 10 *¹*g/g (EF1) for PdG, and 0.5 *¹*g/g (WF1) and 2 *¹*g/g (EF1) for Et for the majority of days (¸60%) on which hormone values are available (medians WF1: 5.9 *¹*g/g for PdG, 0.85 *¹*g/g for Et, *n* D 16; medians EF1: 12.6 *¹*g/g for PdG, 2.7 *¹*g/g for Et, *n* D 16). Yet gaps in sample collection precluded discrimination among separate ovarian cycles. During pregnancy, concentrations of PdG and Et showed a high intra-individual day-to-day variability, with maximum values in both hormones being recorded during mid/late gestation. Both breeding females were subject to male mateguarding behavior, which started with the onset of ovarian activity in April and also occurred at other times in the following months. The behavior was absent in the period of low hormone levels following birth and during pregnancy. In both females and all reproductive conditions fecal PdG and Et concentrations are highly significantly correlated (WF1 (*n* D 129): *r* D 0*:*82; *t* D 15*:*86; *p <* 0*:*0001; EF1 (*n* D 93): *r* D 0*:*86; *t* D 16*:*33; *p <* 0*:*0001).

**Nonreproductive Females**

Group E contained 2 nonreproductive adult females that both presumably emigrated in September. Both females had also been nonreproductive in the previous year. Figure 2 shows the profiles of PdG and Et excretion during the 9-mo period for each of them. Like the hormone profiles of the breeding females, both monkeys exhibited clear fluctuations between low and elevated levels of progestogens and estrogens over the entire study period, indicating ovarian activity. On the majority of days (¸60%) for which hormone values are available, progestogen and estrogen levels exceeded 3 *¹*g/g and 1 *¹*g/g, respectively. Their hormone profiles resemble those of the breeding female of E, both in terms of pattern and overall concentrations, and they differ clearly from the low, baseline levels of the juvenile female (medians EF2: 4.2*¹*g/g for PdG, 1.1*¹*g/gEt, *n* D 49; medians EF3: 7.2 *¹*g/g for PdG, 1.6*¹*g/g for Et, *n* D 67; for WF1, EF1, and EF4, see above). Gaps in sample collection and an intraindividual day-to-day variability in hormone concentrations preclude discriminating individual ovarian cycles for either female. The nonreproductive females were not targets of male mate-guarding. Like findings for the 2 reproductive females, concentrations of fecal steroids are also highly significantly correlated in both nonreproductive animals (EF2 (*n* D 58): *r* D 0*:*82; *t* D 10*:*8; *p <* 0*:*0001; EF3 (*n* D 89): *r* D 0*:*8; *t* D 12*:*28; *p <* 0*:*0001).

**DISCUSSION**

We have provided the first data on the excretion patterns of fecal estrogens and progestogens throughout a complete annual reproductive cycle in breeding and nonbreeding wild female moustached tamarins. The reproductive females experienced a prolonged period of ovarian inactivity after parturition, and nonreproductive females had ovarian activity. Via fecal hormone analysis we monitored female reproductive status and were able to differentiate between phases of ovarian inactivity and activity in individual females (Heistermann *et al.*, 1993;Wasser *et al.*, 1988; Ziegler *et al.*, 2000). However, the incompleteness of samples in combination with a day-to-day variability in hormone levels prevented us from discriminating between individual ovarian cycles within the phases of ovarian activity, and from determining the exact time of conception. Difficulties with sample collection and the occurrence of large gaps between subsequent samples of the same individual were mainly attributable to the arboreal life and the feeding ecology of the species. Moreover, like findings of Sousa and Ziegler (1998) on captive common marmosets, there are significantly higher hormone concentrations in samples collected in the first half (*<*11:00h) than in samples collected in the second half (*>*11:00h) of the tamarin activity period. Although we only used afternoon samples to generate hormone profiles, this did not completely eliminate the intraindividual day-to-day variability in hormone concentrations because part of it seems to be attributable to variation in sample quality, particularly the degree of undigested dietary fiber. Since dietary fiber composition can affect fecal hormone concentrations (Wasser *et al.*, 1993), it is likely that the high and variable proportions of undigested fecal matter increased the variability in excreted hormones (*cf.* Ostner and Heistermann, 2003). Despite the methodological problems, clear changes in the excretion pattern of the progestogen and estrogen metabolites over time in combination with information on parturition dates allowed us to differentiate between phases of ovarian inactivity and ovarian activity, including pregnancy, in the breeding females. The period of ovarian inactivity following parturition in the 2 breeding females lasted for 54 (WF1) and 64–82 (EF1) days. Although comparable data for captive moustached tamarins are not available, the period of postpartum ovarian quiescence is 3–4 times longer than described for other captive callitrichid species (French *et al.*, 2002,). Thus, like wild cotton-top tamarins that experience an average postpartum period of reproductive inactivity of 144 days (Savage *et al*., 1997), a postpartum estrus shortly after parturition did not occur in the 2 breeding subjects. The lack of a postpartum estrus is further supported by a median interbirth interval of 334 days in the EBQB subjects, and interbirth intervals of 8 to 14 mo in other wild populations of moustached tamarins (Soini and Soini, 1990). The factors underlying postpartum ovarian inactivity in wild, but not in captive female callitrichids, are not clear. However, in both EBQB reproductive females, onset of ovarian activity coincided well with increasing independence of the young. Carrying declined after the 54th and 70th day of life in W and E, respectively (pers. observ.) and nursing becomes infrequent by the 7th week of age (Snowdon and Soini, 1988), suggesting that a lack of a postpartum estrus in the wild females might be attributable to higher energetic costs versus the captive situation (Goldizen *et al.*, 1988; Peres, 1994). The influence of energetic constraints on female reproductive function is supported by the study of Savage *et al*. (1997) who found that the range of postpartum reproductive inactivity of 19–200 days in cotton-top tamarins depended on the environmental (feeding) conditions under which they lived (Savage *et al.*, 1996a). Additionally, in captivity, interbirth intervals as short as 174 and 175 days occurred in 2 moustached tamarin females (Villavicencio *et al.*, 1990), suggesting that the postpartum period of ovarian inactivity is considerably shortened under certain favorable circumstances. Further studies using endocrine data as applied here are needed to confirm the general absence of a postpartum estrus in wild moustached tamarins and in other callitrichid species and to elucidate the factors underlying the phenomenon. Although we could not determine the exact time of conception from endocrine data, it probably occurred during the last period of male mateguarding because in primates the behavior usually occurs during female receptive periods (Dixson, 1998). Further, also in the EBQB females, it exclusively occurred during the phase of ovarian activity. Accordingly, gestation length of EF1 was 150–160 days, which compares well with gestation lengths in other tamarin species (*Saguinus fuscicollis*, 150 days: Heistermann and Hodges, 1995; *S. bicolor*, 160 days: Heistermann *et al.*, 1987; contra *S. oedipus*, 184 days: Ziegler *et al.*, 1987a). The hormone profiles (and the overall hormone levels that were similar to those of the breeding female) in the 2 nonreproductive EBQB females clearly suggest ovarian activity in them, though it was not possible to discriminate individual cycles and prove the occurrence of ovulations. However, the endocrine excretion patterns differed considerably from the usually consistently low hormone levels in most nonreproductive captive females of other callitrichid species (Abbott and Hearn, 1978; Evans and Hodges, 1984; French *et al.*, 1984;Kuederling *et al.*, 1995). Moreover, our data compare well with findings on wild nonreproductive female cotton-top tamarins (Savage *et al.*, 1997), common marmosets (Albuquerque *et al.*, 2001), and golden lion tamarins (French *et al*., 2003), which also exhibited elevated progestogen and estrogen concentrations, interpreted as ovarian cyclicity. The reasons for the differences in endocrine patterns between captive and wild nonreproductive females are unclear. Several factors are likely to influence the extent of ovarian inactivity in nonbreeding female callitrichids. For example, agonistic interactions and the effectiveness of potentially reproduction-inhibiting cues emitted by the breeding female could be facilitated in captivity due to closer contact between the monkeys (Epple and Katz, 1984; French and Inglett, 1989; Inglett *et al.*, 1989). Moreover, in contrast to the situation in the wild, nonreproductive captive females usually do not have contact with unrelated males, the presence of which can exert a stimulatory effect on their sexual maturation and ovarian activity (Savage *et al.*, 1996a; Tardif, 1984;Widowski *et al.*, 1990; Ziegler *et al.*, 1987b). Finally, ovarian inactivity in nonbreeding females could be self-imposed and could be understood as a making-the-best-of-a-bad-situation strategy (Saltzman, 2003;Wasser and Barash, 1983):When chances of survival of one’s offspring are low, e. g., due to inbreeding-depression, high likelihood of infanticide, decreased availability of helpers, females can increase their lifetime reproductive success by deferring reproduction until prevailing conditions improve. Accordingly, older females have lower residual reproductive expectation than younger ones, and they should therefore be less likely to defer reproduction (*cf.* French *et al*., 2003). Because at the beginning of our study both nonreproductive females were ¸31 mo old and had contact with extragroup males during intergroup encounters, it is likely that this situation, at least in part, may have stimulated their ovarian activity. Whether our findings reflect a general contrast to the captive situation is unclear in view of the limited data that are available.

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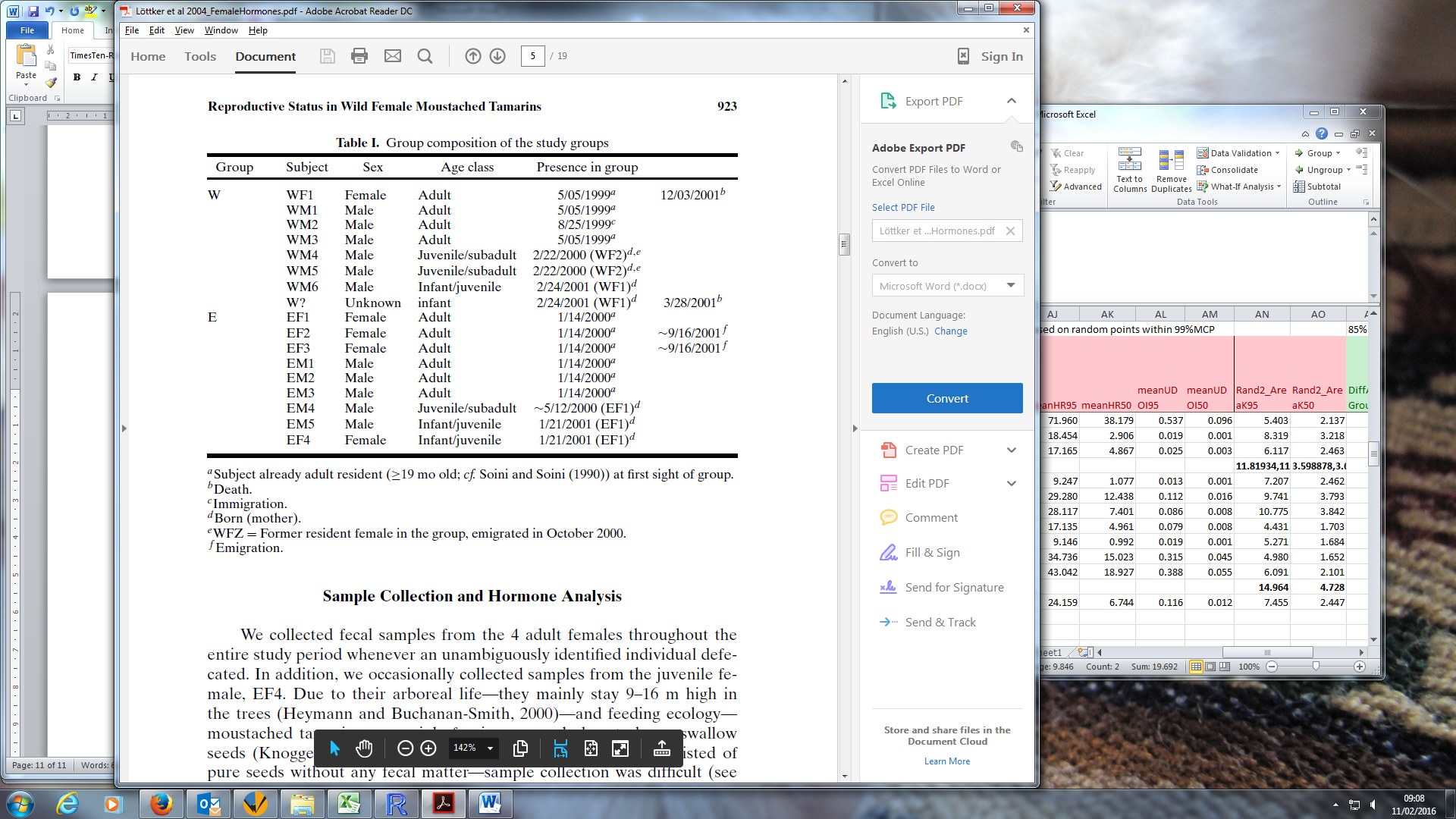
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Tables

**Table I.** Group composition of the study groups



*a* Subject already adult resident (¸19 mo old; *cf.* Soini and Soini (1990)) at first sight of group.

*b* Death.

*c* Immigration.

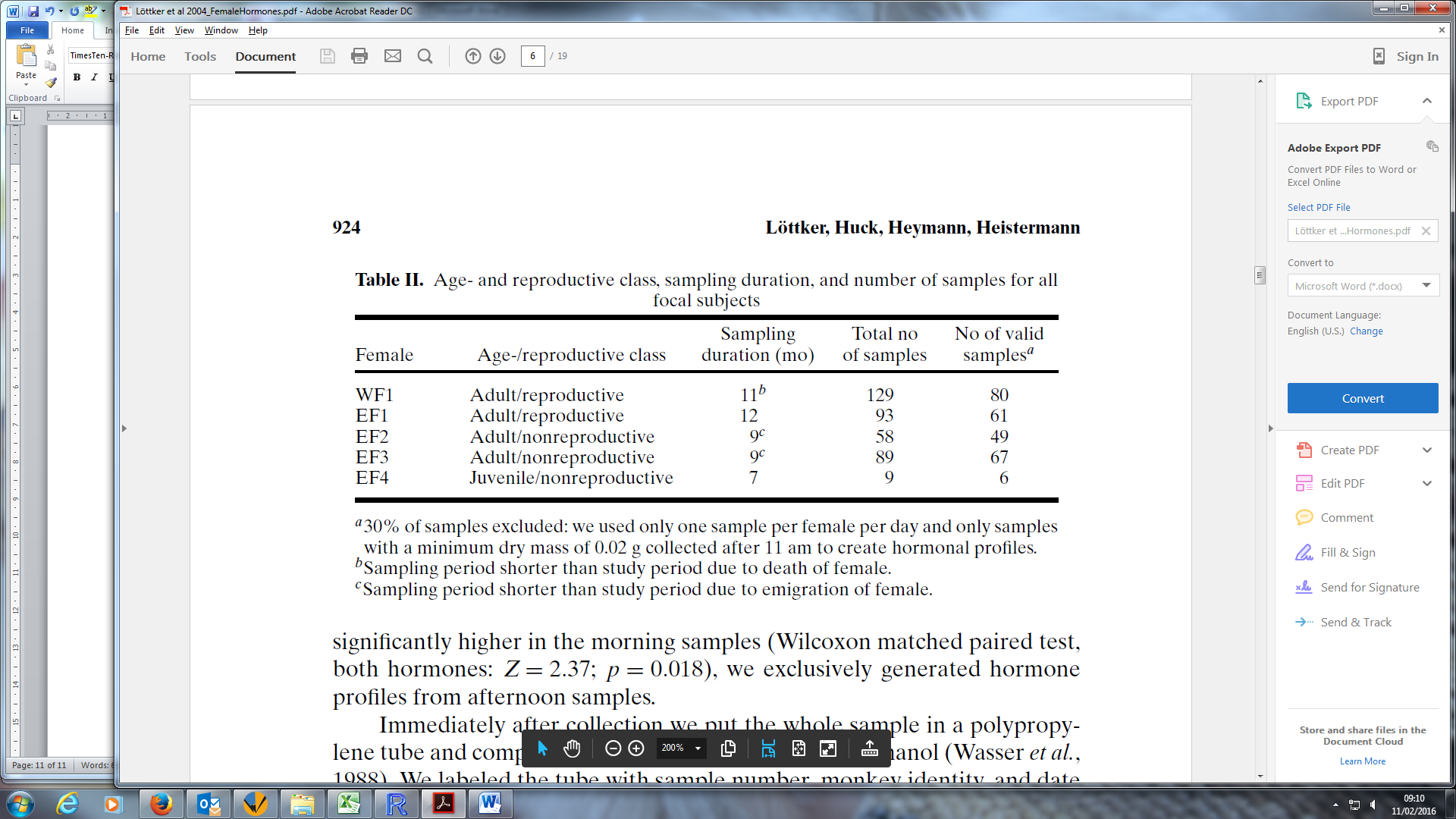
*d* Born (mother).

*e* WFZ D Former resident female in the group, emigrated in October 2000.

*f* Emigration.

**Table II.** Age- and reproductive class, sampling duration, and number of samples for all

focal subjects



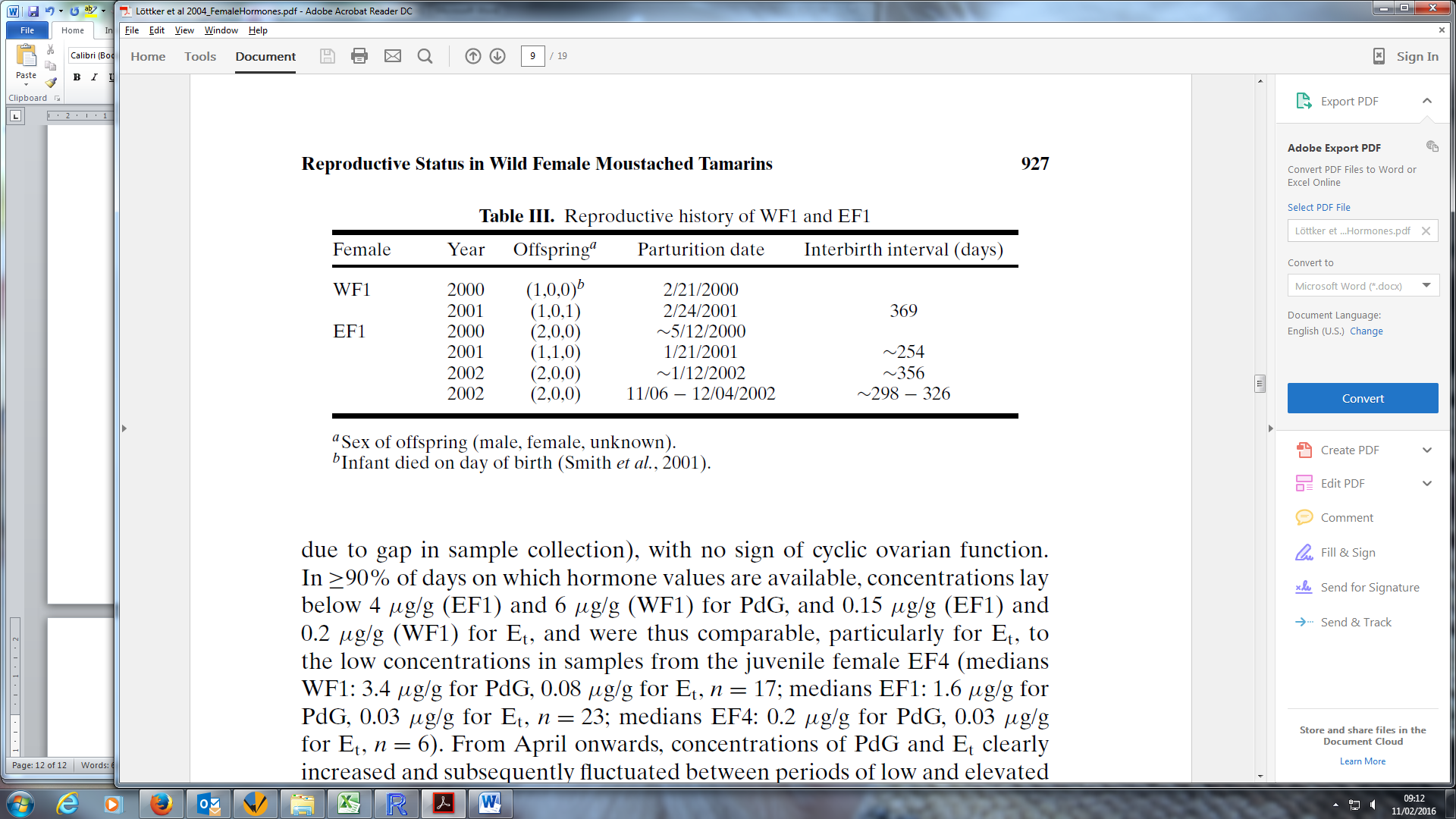
*a* 30% of samples excluded: we used only one sample per female per day and only samples

with a minimum dry mass of 0.02 g collected after 11 am to create hormonal profiles.

*b* Sampling period shorter than study period due to death of female.

*c* Sampling period shorter than study period due to emigration of female.

**Table III.** Reproductive history of WF1 and EF1



*a* Sex of offspring (male, female, unknown).

*b* Infant died on day of birth (Smith *et al.*, 2001).

**Figure legends**

**Fig. 1.** Individual profiles of fecal immunoreactive pregnanediol glucuronide (PdG) and total estrogen (Et) excretion in 2 wild moustached tamarin breeding females of 2 groups during a complete annual reproductive cycle. Arrows indicate the dates of parturition (P), and the date of death of female WF1 (D). The black bars indicate periods of male mate-guarding. Data points separated by *>*3 weeks are not connected by lines. a) female EF1 (group E), b) female WF1 (group W).

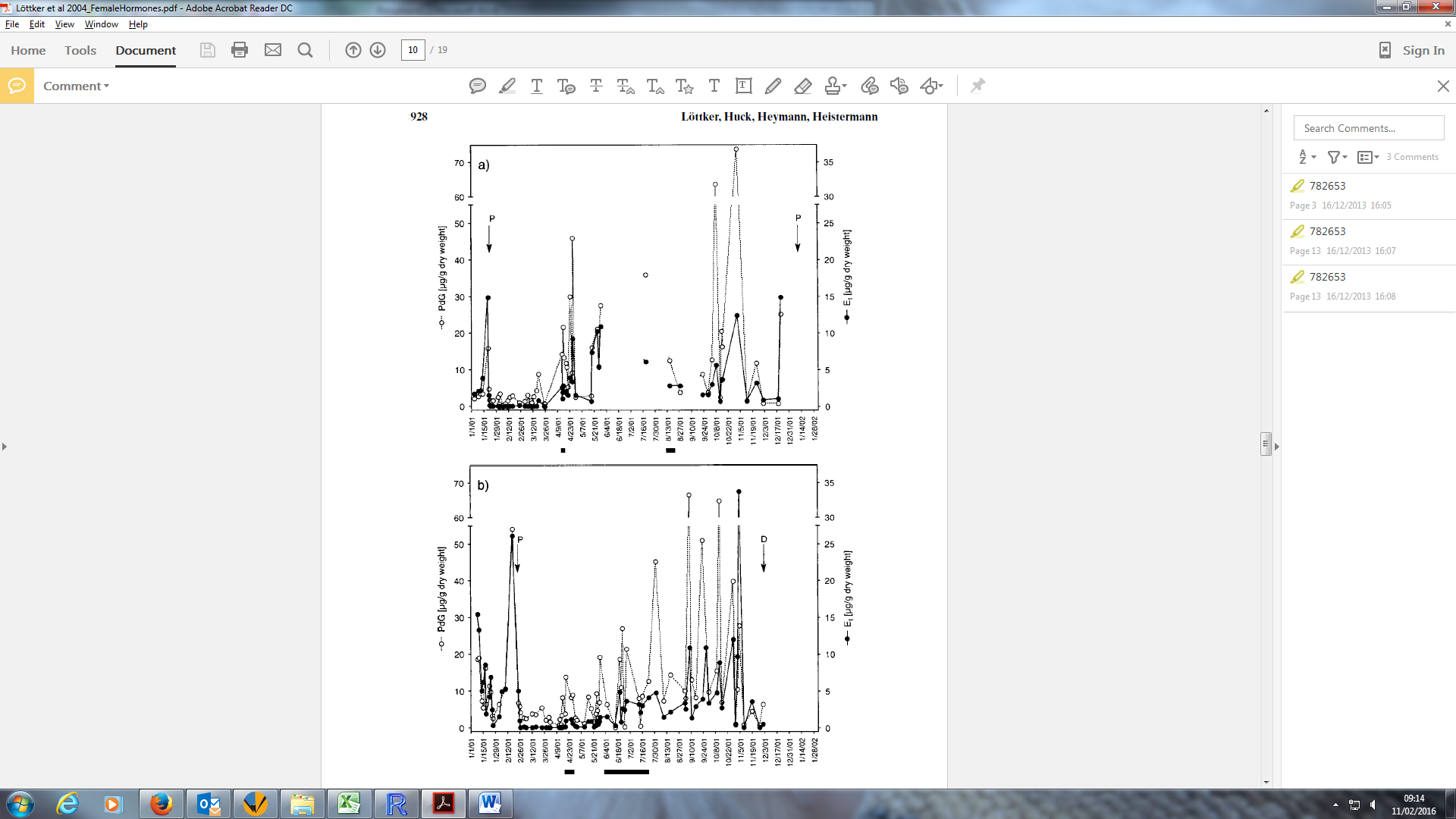
**Fig. 2.** Individual profiles of fecal immunoreactive pregnanediol glucuronide (PdG) and

total estrogen (Et) excretion in 2 nonreproductive adult wild moustached tamarin females

of group E. The arrows indicate the date of emigration (E). Data points separated by

>3 weeks are not connected by lines. a) female EF2, b) female EF3.

**Fig 1**



**Fig 2**

