

Reproductive timing and aseasonality in the sun bear (*Helarctos malayanus*)

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Most species of bears exhibit a reproductive strategy that includes a highly defined breeding season, delayed implantation, pseudopregnancy, and no postpartum estrus. Sun bears (*Helarctos malayanus*), a tropical lowland species, represent a potential departure from the typical ursid reproductive pattern. We studied reproductive timing in captive sun bears by examining fecal hormones and behavior of 13 female and 5 male sun bears, the entire North American population of *H. m. euryspilus* at the time of the study. Fecal estrogens and progestins in females did not vary by season or month, nor did fecal androgens in males. Estrus occurred in 11 of 12 months; breeding and births occurred year-round. However, birth rates were lower in the spring and higher in the fall and winter. Our study documented 1 complete pregnancy, in which delayed implantation did not occur; the delay between estrus and the progesterone rise (i.e., implantation) in the pregnant bear was similar to that seen in nonpregnant bears. All bears, whether nonpregnant or pregnant, exhibited a prolonged period of high progesterone after estrus, indicating obligate pseudopregnancy. Studbook records show that estrus can occur within 6 months after parturition; these cases were typically associated with loss of the previous cub. Our findings suggest that sun bears are unique among ursids, being polyestrous, nonseasonal breeders that do not appear to exhibit delayed implantation and that are capable of initiating estrus in the event of early loss of a cub.

Key words: bears, delayed implantation, estrous cycle, fecal hormones, postpartum estrus, pseudopregnancy, reproductive hormones, seasonality, Ursidae

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Seven of the 8 ursid species are seasonal breeders (5 obligately and 2 facultatively—Spady et al. 2007), despite wide global distributions that span temperate and tropical climates, varied habitats, a 10-fold range in body size, and differing degrees of dietary specialization (Garshelis 2004; Mead 1989; Stirling 1993). These species also typically exhibit delayed implantation, pseudopregnancy, and strictly seasonal timing of estrus (i.e., no postpartum estrus; see below for references). Sun bears (*Helarctos malayanus*), by far the smallest bear, and the only lowland tropical species, appear to be the exception; they breed year-round (Schwarzenberger et al. 2004; Spady et al. 2007; Stirling 1993). Does this species still exhibit the reproductive features of delayed implantation, pseudopregnancy, and lack of postpartum estrus?

Delayed implantation is an arrest in embryonic development that prolongs gestation by months (Sandell 1990). Delayed implantation allows temperate-zone bears to breed and store fat while food is abundant, and then avoid harsh

weather and conserve resources by becoming inactive during a prolonged gestation. This protraction of the breeding cycle allows bears to have mobile cubs when food is again abundant (Stirling 1993). Six of the 8 species of bears give birth 5–10 months (delay + gestation) after breeding, with progesterone not rising until about 2 months before parturition, coincident with implantation (Hellgren et al. 1990; Sandell 1990; Tsubota et al. 1987). Giant pandas (*Ailuropoda melanoleuca*) and sun bears are exceptions to this pattern. In giant pandas, the delay appears slightly shorter, with births occurring after only 4.5 months (Sandell 1990). In sun bears, anecdotal reports suggest a breeding-to-birth interval of approximately 100 days, although one report suggests an interval similar to those seen in temperate bears (reviewed in



Spady et al. 2007). Because there is relatively little hormonal information available for sun bears, we have an incomplete picture of gestation and potential delayed implantation in this species.

Pseudopregnancy is classically defined as the occurrence of any functional luteal phase in a nonpregnant cycle, resulting from the formation of a functional (i.e., progesterone-secreting) corpus luteum after ovulation (following Conaway 1971). Whitney (1967) considered the essential feature of pseudopregnancy to be the persistence of the corpus luteum, such that the luteal phase duration resembles pregnancy duration. Reproductive literature on ursids typically defines pseudopregnancy physiologically, as a hormone profile that is indistinguishable from pregnancy. This has been reported in giant pandas (Monfort et al. 1989), American black bears (*Ursus americanus*—Hellgren et al. 1990; Schulz et al. 2003), Hokkaido brown bears (*Ursus arctos yesoensis*—Tsubota et al. 1987), and Japanese black bears (*Ursus thibetanus*—Sato et al. 2001). There are also indications that pseudopregnancy occurs in sun bears (Frederick et al. 2010; Onuma et al. 2001; Schwarzenberger et al. 2004), warranting further investigation.

The ability to delay implantation is a distinct advantage for seasonally reproducing animals. Postpartum estrus, however, is nearly the antithesis of this strategy. Delayed implantation enables cubs to be born in an appropriate season, but postpartum estrus would result in offspring born off-schedule for key environmental resources. Seasonal breeding often involves highly synchronized mating efforts (Nelson 1995) that pose an array of physiological and social obstacles (e.g., gonadal regression and mate unavailability) to estrus occurring at other times. Although postpartum estrus appears absent in seasonally breeding bear species, these constraints would likely not exist in a nonseasonal breeder. Postpartum estrus could instead represent an adaptive strategy to maximize reproductive rate and not waste further reproductive time. This strategy could be particularly important in the case of neonatal mortality. Classic postpartum estrus occurs routinely after every birth, but in some species may only occur in response to offspring death and cessation of lactation (Bronson 1989). A few reports suggest estrus might occur in sun bears following the death of a cub (e.g., Dathe 1970), but available data are anecdotal.

Sun bears are listed on Appendix I of the Convention on International Trade in Endangered Species, and are categorized by the International Union for the Conservation of Nature as “Vulnerable” to extinction with a “decreasing” population trend (International Union for the Conservation of Nature 2007). Captive breeding efforts in North American zoos have unfortunately met with relatively little success, and the future for the captive population is dire (Faust et al. 2003; Frederick and Shrake 2002). By examining the reproductive patterns of this species, we hope to shed light on possible underlying reasons for this lack of reproduction. Few physiological data on female sun bears exist, and these few available studies had small sample sizes, captive populations outside of North America, and were primarily of mainland sun

TABLE 1.—Sun bear (*Helarctos malayanus euryspilus*) study locations, social groupings, and dates of participation during July 2001 to September 2006.

Location of zoo	Social condition ^a	Study dates
Woodland Park, Washington	0.2	July 2001–December 2005
	1.2 ^b	January 2006–September 2006
San Diego, California	0.2	August 2001–February 2002
	1.2 ^c	May 2003–June 2004
Cleveland Metroparks, Ohio	1.2	October 2003–November 2004
	1.1 ^b	October 2003–November 2004
Lincoln Park, Illinois	1.1	April 2004–April 2005
Audubon, Louisiana	1.1	February 2003–December 2003
	0.2 ^c	December 2003–April 2005
Gladys Porter, Texas	0.2	July 2004–June 2005
St. Louis, Missouri	1.1	August 2004–November 2005

^a 0.2 = 2 females, 1.1 = 1 male and 1 female, 1.2 = 1 male and 2 females.

^b Male moved from Minnesota Zoo to Woodland Park; data were collected on him at both facilities.

^c Male moved from Audubon to San Diego Zoo, no data collected on him while at Audubon; female coming from the Houston Zoo replaced him at Audubon.

bears (Onuma et al. 2001, 2002; Schwarzenberger et al. 2004). We undertook to study the reproductive biology of the entire, recently imported, founder population of the Bornean subspecies of sun bear (*H. m. euryspilus*) captive in North America. This study uses a larger and more detailed data set, including endocrinological analyses, than has previously been available. The 1st part of this study focused on methods of estrus detection, some basic cycle characteristics, and individual female profiles (Frederick et al. 2010). Social influences on reproductive profiles in this species will be considered in a future publication. Our goal in this paper is to analyze reproductive timing and potential seasonal influences on the estrous cycle of the sun bear. We analyzed birth dates, timing of estrus, and longitudinal profiles of fecal hormones to confirm that sun bears are aseasonal breeders, and to examine the potential for pseudopregnancy, delayed implantation, and postpartum estrus in this species.

MATERIALS AND METHODS

Subjects.—The subjects of our study were 5 adult male and 13 adult female wild-caught Bornean sun bears that had been illegally kept as pets prior to being loaned from the Malaysian Government to 8 zoos in the United States (Table 1). These 18 animals represented the entire North American captive population of *H. m. euryspilus* at the time of study. Age estimates ranged from 2 to 19 years. All bears were exhibited and socially housed in seminaturalistic enclosures at latitudes ranging from 30°N to 47°N. Five females were housed with a male throughout the study; 1 female was switched from a male to a female partner, 4 females were introduced to a male during the study period (2 of these females were studied for 6 years; the male arrived in the final year), and 3 were not housed with a male at any point during the study (Table 1). Two adult males were moved to facilities during the study period; data sets for 1 of these males were analyzed separately due to the change in

environment and social partner. The other male was studied only at his 2nd facility. Female cycles also were analyzed separately pre- and post-male arrival. A subgroup of 8 females (5 paired with a male and 3 unpaired) that exhibited estrous cycles during the study (Frederick et al. 2010) were used to evaluate seasonality of estrus and luteal phase activity. One of the females residing at the San Diego Zoo (bear 665) became pregnant during the study. All aspects of animal care and use were in compliance with guidelines approved by the American Society of Mammalogists (Sikes et al. 2011).

Seasonality.—Data on birth trends and postpartum estrus in sun bears across seasons were derived from historical specimen reports (International Species Information System [ISIS] Animal Records Keeping System [ARKS]) provided by the Woodland Park Zoo, and from historical population records (bears from the Asian Mainland and of unknown origin) and more recent studbook records (includes Bornean subspecies) for 92 births (Frederick and Shrake 2002; Shewman 2008). Studbook records were summarized in part using PopLink version 1.3 (Faust et al. 2008).

The geographic location (latitude, climate, and region) of each participating institution was considered for its potential influence on seasonality of hormone metabolite concentrations. No significant patterns were detected (data not shown; see also Spady et al. 2007).

Fecal sampling and hormone assays.—The reproductive cycle of the sun bear was monitored throughout the year via collection of fresh fecal samples from all male and female subjects of *H. m. eurypilus* during 2001–2006 (Table 1). Fecal samples from females were collected on average 3 times a week, and fecal samples from males were collected once a week. A total of 3,868 fecal samples were collected from females (range 113–862 samples per female), and 350 fecal samples from males (10–54 samples per male). Bears were fed either corn or birdseed 4–16 h before sample collection to identify fecal samples by individual. All fecal samples were shipped frozen to Woodland Park Zoo (Seattle, Washington) and held until processing at the Center for Conservation Biology (University of Washington, Seattle, Washington). Samples were stored at -20°C at all stages between collection and final analyses, and were extracted and analyzed within a year of collection; note that fecal hormones are stable at -20°C for at least 2 years (Hunt and Wasser 2003).

We used a methanol vortex method for hormone metabolite extraction. Briefly, a 0.2-g subsample of freeze-dried, sifted, well-mixed feces was vortexed with 2.0 ml of 90% methanol for 30 min and then centrifuged, producing a 1:2 methanol extract containing steroid hormone metabolites (for details see Hunt and Wasser 2003). Female fecal extracts were diluted to 1:320 in assay buffer for total estrogen (TE) analyses, and 1:30 for progestin (P) analyses. Male extracts were diluted to 1:50 for androgen (A) analyses. These dilution levels were chosen to fall close to 50% on the standard curve of each assay, the area of greatest precision. The TE assay, which uses an antibody that binds to several estrogens, was a commercially available 125-I double-antibody radioimmunoassay kit

(total-estrogens kit #140202; MP Biomedicals, Solon, Ohio); the manufacturer's protocol was followed but with all volumes halved. The P and A assays were both in-house 3H radioimmunoassays using antibodies raised against progesterone and testosterone, respectively (progesterone antibody CL#425, Animal Reproduction and Biotechnology Lab, Colorado State University, Fort Collins, Colorado; testosterone antibody #250, Clinical Endocrinology Lab, School of Veterinary Medicine, University of California, Davis, California).

Assay variations were as follows: 10.7% intra-assay variation and 9.3% interassay variation for the TE assay; 4.5% intra-assay and 6.0% interassay variation for the P assay; and 4.4% intra-assay and 2.0% interassay variation for the A assay. Interassay variations are calculated across different batches of assay reagents. For the P and A assays, new standards and controls were made annually and were tested extensively before use to verify that they were indistinguishable from previous standards and controls. The TE assay uses standards that are provided by the manufacturer; these standards change to new lots approximately every year. All samples and standards were run in duplicate; nonspecific binding tubes and blanks were run in quadruplicate. All assays included pooled sun bear controls, and were tested routinely with multiple controls from other laboratories and with aliquots of pooled fecal extracts from several other mammalian taxa.

Sun bear samples were reanalyzed if they had high percent coefficient of variation between duplicates, fell outside the range of the standard curve for that assay, or if assay controls were outside the normal range. In addition, any female TE results that were 2 standard deviations above that individual's mean TE level were rerun to authenticate high estrogen values (i.e., possible estrus). All 3 assays demonstrated good parallelism and accuracy for pooled fecal extracts of sun bears (data not shown). The TE and P assays reliably delineate sun bear estrous cycles using fecal samples (Frederick et al. 2010). See Wasser (1996), Wasser et al. (1994, 1996), and modifications in Rolland et al. (2005) for further assay details and antibody cross-reactivities.

Pseudopregnancy.—Of the 13 females in this study, only 8 exhibited a prolonged luteal phase consistent with pseudopregnancy; the others showed no luteal activity and no evidence of estrus (Frederick et al. 2010). Estrous cycles with a high progesterone stage were deemed nonconceptive (pseudopregnant) if either no mating behaviors were observed despite close scrutiny (5 females) or no male was present (3 females). Of the 8 females that exhibited high progesterone, 1 female that was studied longitudinally for 6 years had 12 documented luteal phases; another bear had 2 luteal phases; and the remaining 6 bears each had 1 luteal phase. Incompletely documented luteal phases (e.g., those ongoing at the start or end of a study period) were not considered in the analyses.

Each female's P and TE data sets were transformed into a series of (within subject) z -scores, and the (+) or (–) values of

these scores used as standardized criteria for determining the onset and termination of high progesterone of the luteal phase (for details see Frederick et al. 2010). The follicular phase began at the end of high progesterone (day after last + P z-score). Estrus was designated as the peak TE value (± 4 days) that preceded the start (1st + P z-score) of the progesterone rise. We assumed that high progesterone indicated ovulation had occurred (Monfort et al. 1989). The delay between ovulation and the progesterone rise (“delay” hereafter) was estimated from the day after peak TE until the 1st + P z-score. Using this method, we could time estrus, the duration of the luteal and follicular phases, and the delay in between.

Delayed implantation.—A breeding-to-birth interval markedly longer than the period of embryological development would indicate delayed implantation. The precise length of the period of embryological development in sun bears is not known. Closely related mammalian species that have young born at a similar stage (i.e., altricial versus precocial) have roughly similar gestation lengths (Martin and Maclarnon 1985; Millar 1981). We used the allometric analyses of Martin and Maclarnon (1985) to estimate the embryological development time for sun bears from gestation lengths for the American black bear and Hokkaido brown bear (approximately 8 weeks—Hellgren et al. 1990; Tsubota et al. 1987) and brown bear (8–10 weeks—Sandell 1990) and female body masses for all 3 species (Stirling 1993). Based on these analyses, sun bears can be predicted to have a period of embryological development falling within 2 weeks of these species and no longer than 90 days (Martin and Maclarnon 1985; Millar 1981). We compared this length to the historical reports documenting known breeding and parturition dates in sun bears. We also examined the delay of the study pregnancy. Finally, the delay observed in the pseudopregnant estrous cycles also was considered for its potential similarity to the delay seen in the study pregnancy, although pseudopregnant cycle data cannot directly be used to assess embryonic diapause.

Postpartum estrus.—Estrus occurring within 6 months after birth would be unusual for any bear species (including sun bears) given the long (>1 year) period of cub dependency seen in all bears (Stirling 1993). We therefore examined all potential cases of estrus occurring within 6 months of a birth, noting whether or not the cub survived. We first identified the 10 studbook records that had the lowest number of days between 2 consecutive births, and then subtracted 95, the lowest number of days that has ever been reported for a sun bear gestation (Dathe 1970). The time remaining after subtraction of this minimum gestation time is the maximum range of time in which estrus could have taken place following the 1st birth.

Data analyses.—We used chi-square to examine the distribution of births, number of cycles, and number of different cycling females by season (March–May [spring]; June–August [summer]; September–November [fall]; and December–February [winter]). For data on hormone metabolite concentrations, we calculated grand means $\pm SE$ (monthly or stage) based on averages from individuals to control for unequal data set sizes (e.g., the P average for luteal stage was

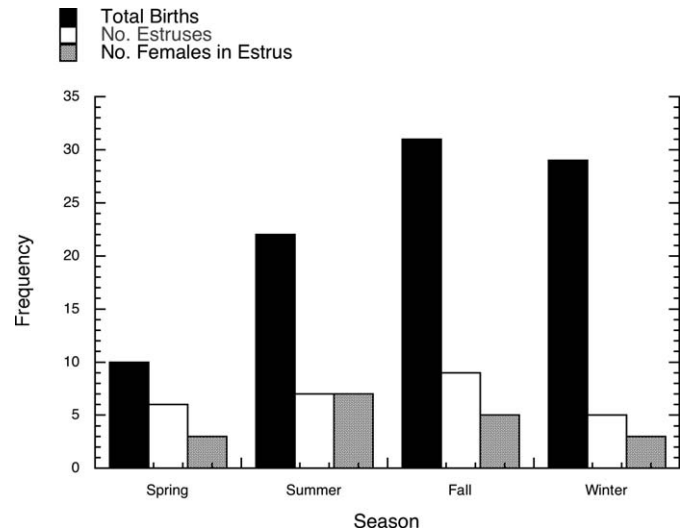


FIG. 1.—Birth totals of the historical population of sun bears including the single Bornean (*Helarctos malayanus euryspilus*) birth from 1942 to 2006 ($n = 92$) and number of estruses and number of different study females in estrus ($n = 8$) according to season.

1st averaged within females and then across females). We then used analysis of variance (ANOVAs) to assess monthly and seasonal differences in P, TE, and A. We next correlated monthly P and TE means with the number of births and TE with births 2, 3, and 4 months later (i.e., the likely range of sun bear gestation length). Finally, we ran correlations between monthly TE and A means. This analysis was further subdivided to examine females designated as the male’s preferred partner (based on behavioral data; data not presented) versus the female designated as dominant (based on caretaker assessments). We ran 2-way ANOVAs testing P and TE concentrations of cycling females during follicular, luteal, and delay stages by season, and duration (days) of these stages by season. All statistical tests used an alpha of 0.05.

RESULTS

Seasonality.—Births occurred in all months of the year. However, there was a significant relationship between births and season ($\chi^2_3 = 11.739$, $P = 0.008$) with birth rates lowest in the spring and highest in the fall and winter (Fig. 1). There were no significant relationships between number of estruses and season ($\chi^2_3 = 1.296$, $P = 0.73$) or number of females in estrus and season ($\chi^2_3 = 2.44$, $P = 0.485$; Fig. 1). Monthly mean P was not correlated with monthly birth rates ($r_{10} = -0.208$, $P = 0.526$). TE also showed no association with birth rates in the same month ($r_{10} = -0.042$, $P = 0.900$), nor with birth rates 2 or 4 months later ($r_{10} = 0.341$, $P = 0.278$; $r_{10} = 0.378$, $P = 0.226$, respectively), but was correlated with birth rates 3 months later ($r_{10} = 0.625$, $P = 0.03$). Mean hormone metabolite concentrations did not vary significantly by month (Fig. 2) or season (respectively) in P ($F_{11,151} = 0.586$, $P = 0.838$; $F_{3,159} = 0.433$, $P = 0.73$), TE ($F_{11,137} = 0.523$, $P = 0.885$; $F_{3,145} = 1.205$, $P = 0.310$), and A ($F_{11,44} = 0.895$, $P = 0.552$; $F_{3,52} = 1.303$, $P = 0.283$). However, monthly mean A

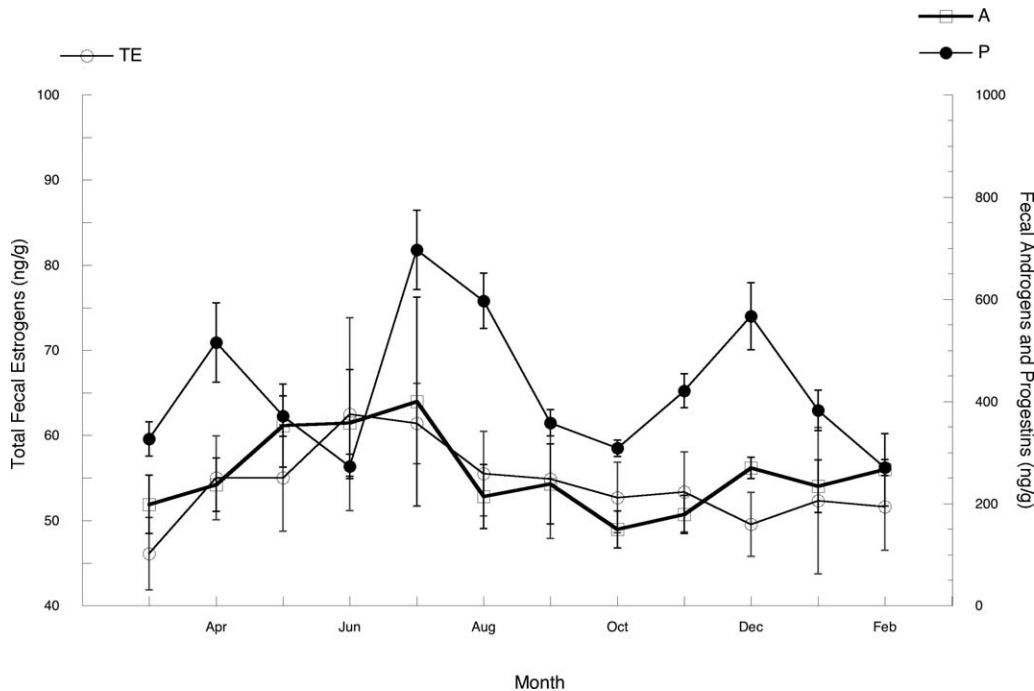


FIG. 2.—Monthly total fecal estrogen (TE) and fecal progesterin (P) in 8–13 female sun bears, and fecal androgen (A) in 6 or 7 males, arranged by season from March (start of spring) to February (last month of winter). Data are shown as mean \pm SE.

of males and TE of females were correlated ($r_{10} = 0.664$, $P = 0.016$; Fig. 2). When males' monthly A concentrations were compared to TE concentrations of their obligate female partner (those housed as pairs) or, for males housed with 2 females, their preferred partner, A was not significantly associated with TE ($r_{31} = 0.284$, $P = 0.110$). The results were the same when the nonpreferred female was used ($r_{36} = 0.258$, $P = 0.119$). Only when the dominant female was used did the association become significant ($r_{37} = 0.334$, $P = 0.037$).

Total estrogen concentrations did not vary by stage ($F_{2,40} = 2.176$, $P = 0.127$) or season ($F_{3,40} = 0.552$, $P = 0.650$) or an interaction between the 2 ($F_{6,40} = 0.361$, $P = 0.899$; Fig. 3). P varied among stages ($F_{2,41} = 12.898$, $P = 0.0001$) and was greatest during the luteal stage, but did not differ by season ($F_{3,41} = 1.881$, $P = 0.148$) or by interaction between the 2 ($F_{6,41} = 1.052$, $P = 0.407$; Fig. 3). Similarly, stage duration (days) varied across stages ($F_{2,41} = 21.95$, $P = 0.0001$) and was again greatest during the luteal stage, but did not differ by season ($F_{3,41} = 1.21$, $P = 0.318$) and there was no interaction effect ($F_{6,41} = 1.34$, $P = 0.260$; Fig. 4).

Delayed implantation.—Woodland Park Zoo specimen reports documented 3 breeding-to-birth intervals with lengths of 103, 109, and 110 days, respectively. The pregnant female in the current study had a breeding-to-birth length of 96 days including a delay of 16 days between peak TE (or 14 days if counted from 1st day of mating) and the onset of the P rise.

Pregnancy and pseudopregnancy.—Nonconceptive cycles were hormonally indistinguishable from pregnancy (see examples in Fig. 5). In the 20 complete nonconceptive estrous cycles studied across both paired and unpaired females, the range of time between peak TE + 1 day (i.e., ovulation

estimate) and the start of the P rise was 5–31 days ($\bar{X} = 15$ days \pm 2.2 SE, and median = 16 days; Fig. 4), consistent with what was observed for the actual pregnancy (see previous section). The duration of high progesterone also was similar between the 2 (Fig. 5). In nonconceptive cycles, high progesterone concentrations persisted for 42–88 days ($\bar{X} = 69 \pm 3.3$ days, mode = 68, median = 68; Fig. 4), as compared to the pregnancy, which was 75 days if measured by the same hormonal criteria, or 83 days if measured until parturition. In the pregnant female, P concentrations decreased 8 days before parturition (Fig. 5b). Nonconceptive cycles and pregnancy also had similar values for P and TE during the period of high progesterone concentrations (Fig. 5). During the pregnancy, mean hormone metabolite concentrations were P = 889 ng/g \pm 206 SD and TE = 59 \pm 7.7 ng/g, consistent with the averages observed for nonconceptive cycles (Fig. 4).

Postpartum estrus.—Subtracting a minimum gestation length (95 days) from the 10 shortest documented interbirth intervals resulted in the following birth-to-estrus intervals: 26, 33, 41, 48, 53, 57, 61, 66, 89, and 137 days. In 7 of these 10 cases, the cub had died ($n = 5$) or been removed for hand-raising ($n = 2$ —Smith 1980). Circumstances for the other 3 cases are unknown. Most deaths occurred within 48 h of birth. Intervals over 60 days were associated with cubs that lived longer or for which there were no data available other than date of birth.

DISCUSSION

Examination of our hormonal data confirms previous reports that captive sun bears are nonseasonal breeders (Garshelis 2004; Spady et al. 2007). Examination of our data

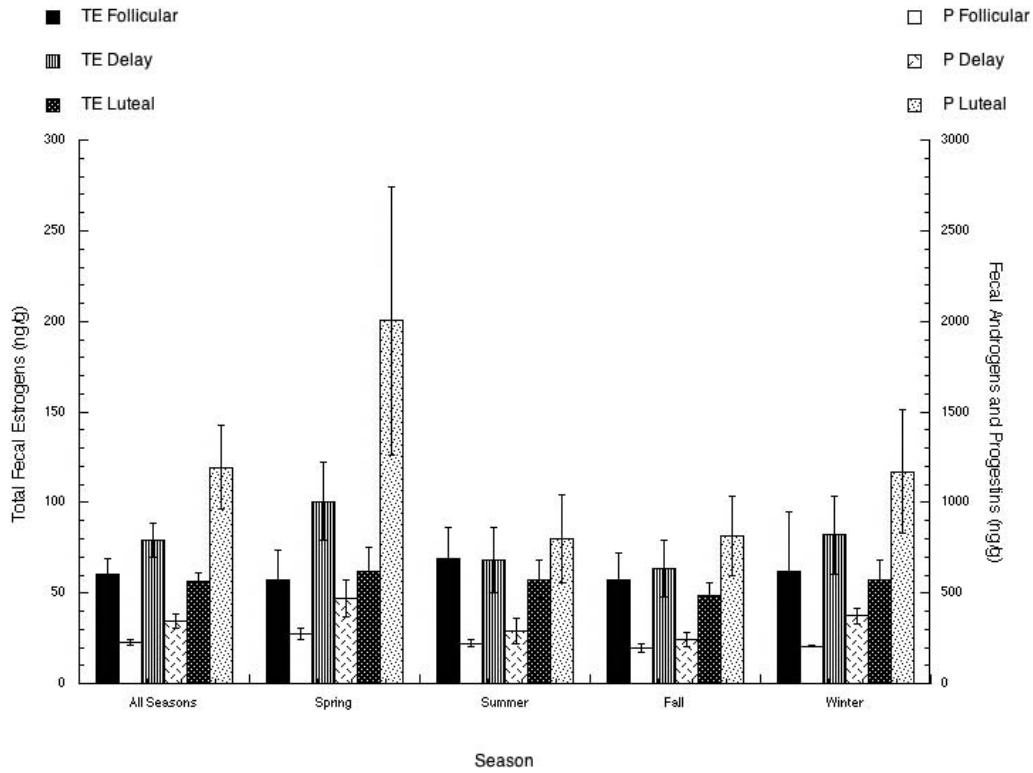


FIG. 3.—Endocrine profiles of total fecal estrogens (TE) and fecal progestins (P) during follicular, delay, and luteal phases of the sun bear's cycle for all seasons combined and by individual season. Data are shown as mean \pm SE.

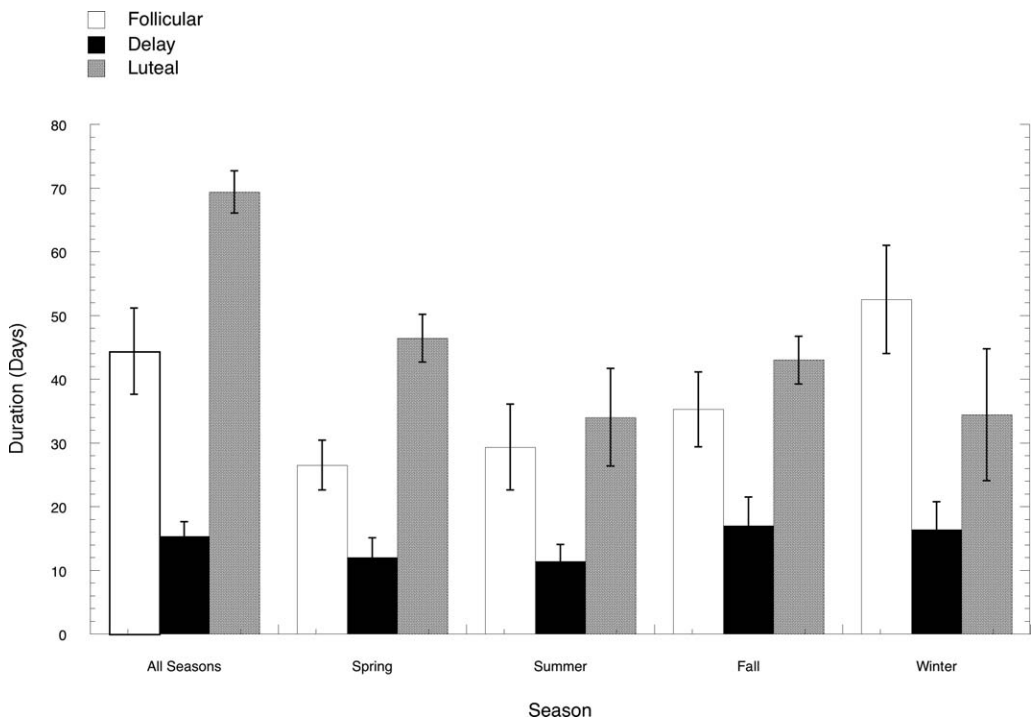


FIG. 4.—Mean duration in days \pm SE for follicular, delay, and luteal phases of the sun bear's cycle for all seasons combined and by individual season.

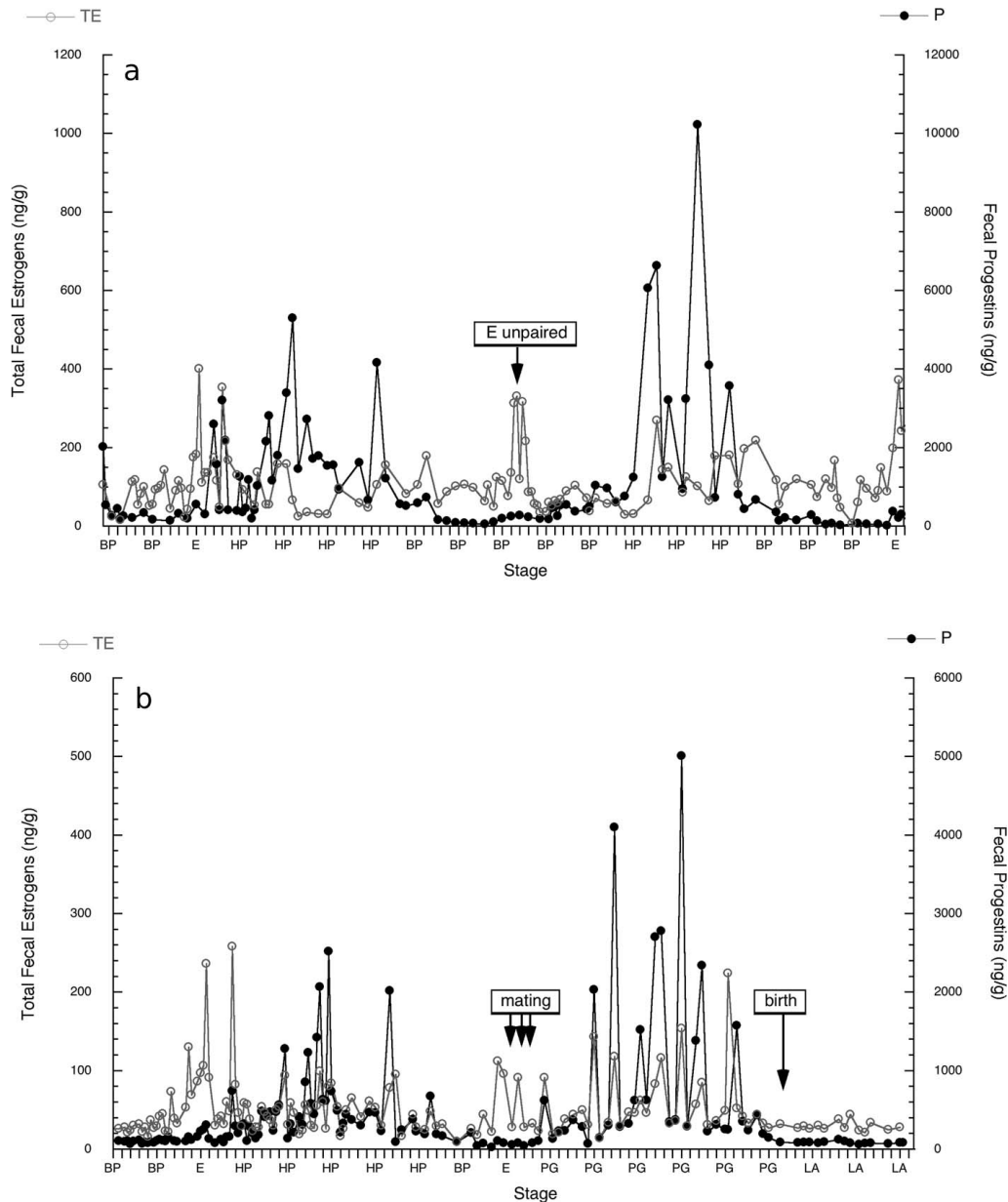


FIG. 5.—Endocrine profiles of total fecal estrogens (TE) and fecal progesterins (P) in pseudopregnancy compared to pregnancy in a sun bear. a) Two consecutive pseudopregnancies in an unpaired female; b) a pseudopregnancy followed by a pregnancy in a different (paired) individual (BP = baseline progesterone [follicular/delay], HP = high progesterone [luteal], E = estrus, PG = pregnant, LA = lactation). Both graphs represent 275 days total; each tic mark on the x-axis equals 3 days.

suggests that sun bears do not exhibit delayed implantation, but do routinely exhibit true pseudopregnancy, and are capable of initiating estrus following neonatal mortality. Thus, broadly speaking, sun bears appear to be unlike other bears in all aspects except pseudopregnancy.

The lack of seasonality in P or TE concentrations and durations of follicular, luteal, and delay stages of the cycle corroborate and extend previous findings (see Schwarzenberger et al. 2004; Spady et al. 2007). Our results confirm that unlike the other 7 bear species, nonpregnant sun bears are routinely polyestrous throughout the year.

If female sun bears are receptive year-round, then males should not show gonadal regression and recrudescence patterns.

In seasonally reproducing American black bears (*U. americanus*), testicular recrudescence is initiated in January and ends in May (Howell-Skalla et al. 2000). A corresponding rise in male testosterone in the spring has been documented in both male American black and polar bears (*Ursus maritimus*—Foresman and Daniel 1983; Garshelis and Hellgren 1994; Palmer et al. 1988). Although we did not measure testicular size directly in this study, male androgen data did not show a seasonal pattern. Male androgen levels were instead associated with female estrogen levels across months and seasons, following the females' nonseasonal fluctuations. Males that were paired with 2 females appeared to be most influenced by the dominant female. This social rather than seasonal pattern

agrees with previous male sun bear findings (Hesterman et al. 2005) and fits with more general observations that in nonseasonal breeders, social cues can be as important as environmental cues (Wingfield and Kenagy 1991).

In contrast to the nonseasonal pattern seen in hormones, births of captive sun bears in North America occurred most often in fall or winter. This mild peak in historical births was correlated with a mild elevation in study female TE 3 months earlier. The pattern of a fall–winter peak in births suggests either a timing similarity with temperate bears (Garshelis 2004; Spady et al. 2007), or that spring and summer estrous cycles are more likely to be conceptive. Birth patterns in wild sun bears show a similar trend. During a 2-year study in East Kalimantan, Borneo, more cubs were born during the wet season ($n = 11$) from November to April than during the dry season ($n = 7$) from May to October (Schwarzenberger et al. 2004). Species that breed year-round may still show birth peaks that reflect conditions favoring conception and food availability during weaning (e.g., wild yellow baboons [*Papio cynocephalus*]—Wasser 1996). Although this seasonal trend in sun bear births is subtle compared to the obvious seasonality seen in other bear species, it does suggest that sun bears may be sensitive to some seasonal environmental cues.

The sun bear's lack of strong seasonality is likely related to its habitat. Temperate bears typically live where there are distinct seasonal changes in food abundance. The habitat of the sun bear is the lowland tropical hardwood forests of mainland Southeast Asia, Sumatra, and Borneo (Servheen 1999), which are weakly influenced by 2 monsoon seasons (Wong et al. 2004). Examination of field data indicates that sun bears (unlike other bears) do not have seasonal shifts in diet and are active year-round (Wong et al. 2002). But sun bears are strongly affected by variable fruiting events, droughts, and fires, all of which can make the productivity of these forests limited and unpredictable (Fredriksson 2005; Fredriksson et al. 2006; Wong et al. 2002). This situation could exert a keen selective pressure on sun bears to be opportunistic rather than seasonal in their reproductive strategies.

Seasonally breeding bears should, in theory, avoid postpartum estrus whether or not cubs survive. This timing of estrus would result in births that would be asynchronous with seasonal events and food resources. Our data analyses showed that 9 of 92 recorded captive sun bear births resulted from an estrus that occurred within 6 months of the birth of the previous cub. The majority of these cases involved the death or removal of the 1st cub (removal likely due to maternal neglect—see Smith 1980). There is no evidence that postpartum estrus occurs in this species if a cub is healthy and the female lactates, but sun bears clearly can initiate estrus if cubs are lost shortly after birth.

Sun bears appear to have a more flexible reproductive strategy than other bears, which may allow them to quickly begin a new pregnancy when necessary. Of the 2 facultatively seasonal bear species (following Spady et al. 2007) that might be expected to display postpartum estrus, studbook records for the Andean bear (*Tremarctos ornatus*) had only 4 possible

cases of postpartum estrus out of 203 births (M. Connolly, Tulsa Zoo & Living Museum, Tulsa, Oklahoma, pers. comm.) and records for the sloth bear (*Melursus ursinus*) showed none, even after death or removal of the cub (D. Thompson, Little Rock Zoo, Little Rock, Arkansas, pers. comm.).

The timing of estrus after cub loss suggests another similarity between pregnancy and pseudopregnancy in sun bears. When cub loss occurred immediately after birth (within 24–48 h), estrus onset resembled the timing seen after nonconceptive cycles. The mean interestrus interval for nonconceptive cycles is 115.7 days \pm 6.3 SE (range of 101–131 days—Frederick et al. 2010). Pregnant females who lost a cub soon after birth initiated their next estrus with approximately this same timing, that is, as if they had been pseudopregnant rather than pregnant.

Examination of our data indicates that sun bears routinely experience pseudopregnancy that is hormonally indistinguishable from a true pregnancy. This observation is consistent with other bear studies that also have reported an absence of detectable differences in either hormone profiles or duration between the 2 (Sato et al. 2000; Schulz et al. 2003; Tsubota et al. 1987). Schwarzenberger et al. (2004) also reported cycles in sun bear females that appeared similar to pregnancy yet did not result in parturition, but these females were paired with males so fetal loss, although unlikely, could not be ruled out. Onuma et al. (2001) documented 2 cases of unpaired sun bears that exhibited pseudopregnancy complete with lactation. During periods of high progesterone concentrations, pseudopregnant sun bear females have significantly increased appetite and decreased social and affiliative behaviors (Frederick et al. 2010), reminiscent of pregnant bear behavior (Stirling 1993). Pseudopregnant females also have been observed to routinely excavate dens during this stage of the cycle (C. Frederick, pers. obs.). An important management consequence of pseudopregnancy is that, at present, neither fecal hormone assays nor behavioral measures can reliably detect pregnancy in this species.

In the current study, every documented estrus was followed by approximately 2 months of high progesterone concentrations. As the 3 peaks in our monthly progesterone averages hint, sun bears have up to 3 estrous cycles a year (Frederick et al. 2010; Smith 1980; Spady et al. 2007). One-third of the females in this population never showed estrus. In these acyclic females, estrogen patterns were random, progesterone stayed low, and behavior and other physiological measures confirmed the absence of estrus (Frederick et al. 2010). Thus, all nonconceptive estrous cycles that we present indicate that sun bears obligately show pseudopregnancy (Frederick et al. 2010).

The average delay to the onset of high progesterone concentrations seen in our pseudopregnant bears was almost identical to that seen in the pregnant study female. Other studies comparing pseudopregnant and pregnant bears also found an equivalent delay (albeit of longer duration) in both groups (Sato et al. 2001; Tsubota et al. 1987). Pseudopregnancy in sun and other bears might be an evolutionary side effect of physiological mechanisms that evolved to support delayed implantation, specifically, selection for a persistent

corpus luteum (Spady et al. 2007). Bears that exhibit delayed implantation have a corpus luteum that persists through the months of embryonic diapause (Foresman and Daniel 1983; Mead 1989; Schulz et al. 2003; Tsubota et al. 1987). Nonconceptive cycles, and hence pseudopregnancy, are presumably rare in wild bears. Therefore, there would be little active selection against pseudopregnancy (following Conaway 1971), which may explain how sun bears could retain pseudopregnancy and yet still potentially lose delayed implantation.

We found no evidence to suggest that sun bears have delayed implantation, despite its being a key mechanism of the seasonal reproductive strategy in other ursids (Mead 1989). The relatively short breeding-to-birth intervals reported in this paper contradict those of McCusker (1973), who reported sun bear gestations of 6–8 months. Our gestation lengths align with previous sun bear reports of 95–96 days (Dathe 1970), and 101, 105, and 96 days (Smith 1980). The breeding-to-birth lengths presented in this study, including the 1 pregnancy, are only slightly greater than the 90-day limit suggested by Martin and Maclarnon's (1985) model for duration of embryological development, and the high progesterone duration of the pregnancy fell well within the model's predicted range.

Delayed implantation in other bears is about 3–7 months (see "Introduction"). The present study's pregnant female showed a P rise only 2 weeks after mating and the pregnant sun bear in the study of Schwarzenberger et al. (2004) exhibited a P rise 1 month after mating. These limited data showing a small delay of ≤ 1 month contradict the characterization of sun bears as having delayed implantation like that of other ursids (Mead 1989).

Sun bear reproductive flexibility may represent an adaptation to an environment with weak seasonal cues and unpredictable food availability. We speculate that the sun bear reproductive cycle may therefore be relatively easily disrupted when conditions are not ideal. In the wild, sun bears face both natural and anthropogenic disturbances. In captivity, they face alternate stressors including constant sociality, lack of control, and close proximity to humans. These and other artifacts of a captive life are known to negatively impact reproduction in a variety of species (Lindburg and Fitch-Snyder 1994). We see possible evidence for this sensitivity to disruption in the poor reproductive track record of captive sun bears. In sum, the reproductive flexibility exhibited by sun bears may unfortunately make them more vulnerable to disturbance than other bears.

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