



## Timing is everything: expanding the cost of sexual attraction hypothesis



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Anthropogenic disturbances present challenges to animals. Behavioural plasticity is one way that animals adjust to degraded habitats. In the present study, we examined how ecological conditions impact reproduction of female red colobus monkeys, *Procolobus rufomitratus*, in Kibale National Park, Uganda. Wrangham (2002, *Behavioural diversity in chimpanzees and bonobos*, pp. 204–215) proposed the ‘cost of sexual attraction’ hypothesis to explain the relationship between ecology and female reproduction. Here for the first time we test and expand on this hypothesis in a folivorous species, the red colobus monkey. We compared four groups of red colobus, two in previously logged areas and two in old-growth areas, to examine differences in female reproductive behaviours and physiologies. We predicted that, because of differences in food availability, females living in logged areas would (1) have a shorter duration of genital tumescence, (2) mate less frequently and (3) constrain mating behaviours more to periods of maximal genital tumescence compared to females in old-growth areas. As predicted, females in logged areas were fully tumescent for a significantly shorter period, copulated significantly less frequently and showed mating behaviours when fully inflated significantly more than females in old-growth areas. This behavioural plasticity contributes to the maintenance of female reproductive function in the face of environmental constraints associated with anthropogenic disturbance that influences food resources.

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Behavioural plasticity is one type of phenotypic plasticity (the differential expression of a trait in response to environmental influences; Schlichting & Pigliucci, 1998) and is thought to be an important adaptation (West-Eberhard, 2003), particularly for individuals inhabiting variable environments (Brashares & Arcese, 2002; Dingemans, Kazem, Réale, & Wright, 2010; Komers, 1997). One form of behavioural plasticity, flexible mating behaviours, may be particularly important for females that are often subordinate to males. Female primates are notable in that their mating is often not confined to ovulation, but occurs over an extended time frame (Hayssen, Van Tienhoven, & Van Tienhoven, 1993; Hrdy & Whitten, 1987; Loy, 1987; Struhsaker, 1997). These nonreproductive mating behaviours serve a number of purposes, such as infanticide avoidance (Knott, Emery Thompson, Stumpf, & McIntyre, 2010; van Noordwijk & van Schaik, 2000), promoting ‘friendships’ (Palombit et al., 2000; Palombit, Cheney, & Seyfarth, 2001; Smuts & Smuts, 1993) and improving access to food (Gomes & Boesch, 2009).

Female primates use a variety of strategies to maximize reproductive success (Stumpf, Martínez-Mota, Milich, Righini, & Shattuck, 2011). For example, females benefit from mating with multiple males over their cycle, but selectively mate with preferred males during periovulatory periods (Stumpf & Boesch, 2005). Mating with multiple males may be an important strategy to promote paternity confusion and avoid infanticide (Hrdy, 1979; Palombit et al., 2000; Smuts & Smuts, 1993).

Increased behavioural plasticity may be especially important for individuals facing energetic constraints because it allows them to adjust to these conditions and maintain reproductive function (Estrada & Coates-Estrada, 1996; Marsh, 2003; Rodríguez-Luna, Domínguez-Domínguez, Morales-Mávil, & Martínez-Morales, 2003; Silver & Marsh, 2003). Ecological stressors are found to correlate negatively with reproductive fitness in a number of species (Altmann & Alberts, 2003; Bercovitch, 2001; Berger, Ward Testa, Roffe, & Monfort, 1999; Emery Thompson, Kahlenberg, Gilby, & Wrangham, 2007; Knott, 1999; Lipson, 2001). Maintaining a positive energy balance is particularly important for females because of its close relationship to ovarian function, pregnancy maintenance and lactation (Ellison, 1990; Emery Thompson & Wrangham, 2008; Miller, Bales, Ramos, & Dietz, 2006; Sherry, 2002; Tardif, Ziegler, Power, & Layne, 2005; Wade & Schneider,

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1992). Different species have different strategies to deal with reproductive energy demands, such as seasonally breeding sifakas, *Propithecus verreauxi*, which give birth during periods of low food availability and wean during periods of the highest food availability (Lewis & Kappeler, 2005), or hanuman langurs, *Presbytis entellus*, which conceive in the time of best nutritional status and give birth and wean during periods of low food availability (Koenig, Borries, Chalise, & Winkler, 1997). Even within a species, environmental variability can cause variation in life history traits (Blanck & Lamouroux, 2007; Boyd, 2000). Both crabeater seal, *Lobodon carcinophagus*, and grey seal, *Halichoerus grypus*, mothers rely on energy stores for successful reproduction; thus, environmental conditions, including food availability, influence the life history characteristics of individuals in these species (Boyd, 2000). Similarly, Blanck and Lamouroux (2007) found that variation in environmental conditions resulted in greater variation between populations than between species in growth rate, mortality rate and length of breeding season for 25 species of European freshwater fish.

Building on previous research on how ecological conditions affect female reproductive physiology and sexual behaviours (Clutton-Brock & Harvey, 1978; Crook, Ellis, & Goss-Custard, 1976), Wrangham's (2002) cost of sexual attraction hypothesis argued that habitat quality was the reason for the difference in oestrus length and mating rates in the genus *Pan*. Two important characteristics of *Pan* are that females have genital swellings that become maximally tumescent around ovulation and that the members of this genus live in fission–fusion societies. Wrangham (2002) argued that maximally tumescent females attract males, which effectively increases their subgroup size and, subsequently, feeding competition. Thus, Wrangham (2002) argued that females in low-quality habitats cannot afford to associate with large parties, so fewer reproductive cycles and limited time for mating would be advantageous. This pattern should result in high mating rates over fewer cycles and could be seen through shorter periods of maximal tumescence and increased daily copulation rates (see Deschner & Boesch, 2007 for a refinement). Wrangham used published data for eastern and western chimpanzees and bonobos to provide evidence for this idea, but he never collected novel data to test his hypothesis.

Here we expand on Wrangham's cost of sexual attraction model by testing it in another species, and we provide the first systematic field test of the hypothesis. We examined four groups of red colobus monkeys, *Procolobus rufomitratus*, including two occupying previously logged forest and two occupying old-growth forest, to determine whether females living in degraded habitats minimize the cost of sexual attraction by limiting their mating behaviour to the time when they are most likely to conceive. Similar to females in the genus *Pan*, female red colobus have perineal swellings that fluctuate in size over the course of their cycle (Struhsaker, 1975; Struhsaker & Leland, 1987). Copulations occur through the year (Struhsaker, 1997), and females mate with multiple males throughout their cycle, including when they are not tumescent (Starin, 1991; Struhsaker, 1975, 2010; Struhsaker & Leland, 1985). Based on Wrangham's (2002) hypothesis, we tested three hypotheses: females in logged versus old-growth habitats (1) have a shorter duration of maximal tumescence, (2) mate less frequently and (3) constrain their mating more to maximal tumescence.

## METHODS

We conducted research in the forest near Makerere University Biological Field Station (MUBFS) in Kibale National Park, Uganda (hereafter Kibale; 795 km<sup>2</sup>; 0°13'–0°41'N, 30°19'–30°32'E). Kibale is a mid-altitude, moist evergreen forest that receives 1696 mm of

rainfall annually (Chapman & Lambert, 2000; Stampone, Hartter, Chapman, & Ryan, 2011). Kibale provides a valuable setting for examining the impact of habitat disturbance on foraging strategies because of the diversity of habitats and the extensive long-term ecological records. Forestry compartment K-30 is old-growth forest that has never been logged (Chapman, Struhsaker, Skorupa, Snaith, & Rothman, 2010; Struhsaker, 2010), whereas K-15 was heavily logged with 50% of the trees either cut or indirectly killed (Chapman & Chapman, 1997, 2004; Kasenene, 1987; Skorupa, 1988; Struhsaker, 1997). The K-13 area was heavily logged, and unwanted tree species were poisoned with arboricide (Oates, 1999). These logged areas are still highly degraded and large canopy gaps persist (Gebo & Chapman, 1995; Lawes & Chapman, 2006). Four tree species (*Pouteria altissima*, *Lovoa swynnertonii*, *Strombosia scheffleri* and *Parinari excelsa*), in which red colobus in old-growth forest at Kibale spend approximately 25% of their feeding time (Struhsaker, 1978, 1997), are also considered high-value timber and were heavily targeted during logging operations (Kingston, 1967). The impact of previous logging activities on differences in overall tree densities and food availability between logged and old-growth areas has been previously documented by Kibale researchers (Chapman et al., 2010; Snaith & Chapman, 2008; Struhsaker, 1997). Furthermore, in this study population, females spend significantly more time feeding in logged areas than in old-growth areas (Milich, Stumpf, Chambers, & Chapman, 2013).

Red colobus monkeys are a valuable species for investigating primate responses to habitat disturbances because they are highly endangered (Struhsaker & Leland, 1987) and affected by ecological stressors, such as living in areas with low food availability (Chapman et al., 2006; Gillespie & Chapman, 2006). Moreover, multiple groups can be studied in a relatively small area. Red colobus groups are patrilinear and males form a loose dominance hierarchy (Korstjens, 2001; Miyamoto, Allen, Gogarten, & Chapman, 2013; Struhsaker & Leland, 1979, 1987). Unlike other colobines, female red colobus typically transfer from their natal groups (Korstjens, 2001; Struhsaker & Leland, 1979, 1987). Most of what is known about red colobus reproductive parameters comes from Kibale and Abuko in the Gambia (Starin, 1991; Struhsaker, 2010), where both sites show similarities in interbirth intervals, menstrual cycle length and age at sexual maturity (Table 1).

Data were collected on four red colobus groups: two groups in previously logged areas of K-15 and K-13 and two groups in the old-growth area of K-30. These groups were selected because their home ranges were within the logged or old-growth areas and did not overlap with other forest compartments. Each focal group was followed from 0800 to 1600 hours 6 days a week (Table 2) by assistants trained on the research protocol (two people per group per day) that rotated between groups and participated in regular interobserver reliability tests to ensure standardization of data collection. Five focal females (adult, parous females without infants) were selected in each group and observed on a rotating basis

**Table 1**

Demographic information for red colobus at Kibale National Park, Uganda and Abuko Nature Reserve, The Gambia

Trait	Kibale National Park	Abuko Nature Reserve
Interbirth interval	25.5±5.1 months*	29.4 months†
Gestation length	4.5–5.5 months‡	5.25 months‡
Menstrual cycle length	Unknown	27.7 days‡
Age at sexual maturity (males)	35.4–58 months*	≥28 months‡
Age at sexual maturity (females)	38–46 months*	34.25 months‡

\* Struhsaker & Leland (1987).

† Starin (1991).

‡ Struhsaker (1975).

**Table 2**  
Group compositions for the four research groups of red colobus monkeys

	Logged group 1	Logged group 2	Old-growth group 1	Old-growth group 2
Adult males	8	4	9	11
Adult females	22	14	15	22
Subadults	3	3	2	4
Juveniles	8	10	1	23
Infants	10	6	7	13
Total	51	37	34	73

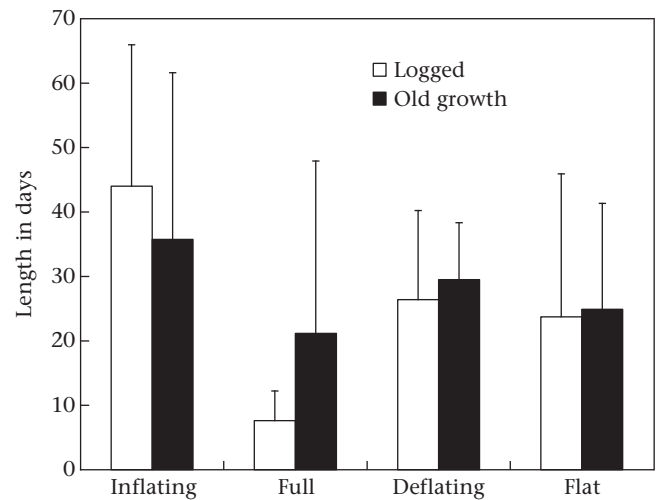
until they gave birth, at which time we chose a new adult female without an infant to enter the rotation, so that at each point in time, data were obtained from five females per group. Because target females changed observational status depending on whether they gave birth, the sample size of focal females for each group differs. Females were identified using individual characteristics such as curve of the tail, scars and fur coloration. The animals were not marked or in any way harmed during the research. We spent 8 months slowly habituating these groups to our presence to ensure that they were not stressed by our presence. We also used this time to choose focal females based on adult females that we saw wean infants prior to the start of data collection. All-day focal follows were conducted on one female in each group per day. All-occurrence data were collected for all mating behaviours for the focal females being observed each day. Using all-occurrence data instead of ad-libitum data reduces the chances of miscalculating mating rates due to poor visibility in areas with high canopies and/or in larger social groups. The anogenital region of each focal female was characterized daily based on Starin's (1991) classifications: inflating, fully swollen, deflating and flat. A total of 27 focal females (15 logged, 12 old-growth) were observed over approximately 4600 h between September 2009 and May 2010.

The durations (in days) of swelling phases (inflating, deflating, fully inflated and flat) were recorded, checked for normality and compared using a *t* test. Copulation rates were calculated by dividing the number of copulations by the number of observation days for each female. Results were standardized by the number of adult males per group and log transformed. (Males mated in similar frequencies, and there was no clear preference for particular males.) Females in logged areas were compared to females in old-growth areas using an ANCOVA, with number of males per group as the covariate. Sexual behaviours (copulations, genital presentations to males, genital inspections by males and grooming males) were tallied during each phase of genital swelling: inflating, fully inflated, deflating and flat. The number of behaviours seen in each phase was then divided by the total number of mating behaviours for each female to calculate the percentage of mating behaviours during each genital swelling phase and to take into consideration the variation in observed mating behaviours for individual females. Because the results were not normally distributed, we compared the percentages of mating behaviours during each phase between logged and old-growth areas using a Wilcoxon two-sample test. All statistical tests were run in SAS and significance levels were set at 0.05.

## RESULTS

### Sexual Swelling Duration in Days

Sexual swelling lengths differed between females living in logged and old-growth forest (Fig. 1). Durations of maximal tumescence were shorter for females in logged areas ( $t_8 = -1.90$ ,  $P = 0.047$ ) than for females in old-growth areas. Females in logged



**Figure 1.** Mean  $\pm$  SD swelling phase durations (in days) for female red colobus monkeys in logged and old-growth areas of Kibale National Park.

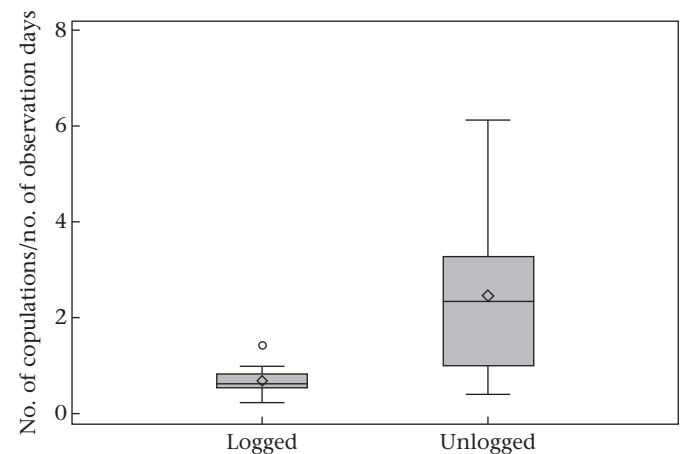
and old-growth areas did not differ in the amount of time they were inflating ( $t_{12} = 0.25$ ,  $P = 0.810$ ), deflating ( $t_4 = 0.17$ ,  $P = 0.870$ ) or flat ( $t_4 = -1.00$ ,  $P = 0.374$ ).

### Copulation Rates

In both habitat conditions, copulations occurred through the year and sexual behaviours most frequently occurred during maximal swelling. However, females in logged areas copulated less frequently overall and were less variable in their copulation frequencies than females in old-growth areas ( $t_{10.412} = -3.64$ ,  $P = 0.004$ ; mean  $\pm$  SD copulations/number of observation days: logged:  $0.70 \pm 0.29$ ; old growth:  $2.47 \pm 1.60$ ; Fig. 2).

### Mating Behaviours in Different Swelling Phases

On days when females did copulate, females in logged areas copulated at higher frequencies (mean  $\pm$  SD:  $1.9 \pm 0.37$  copulations/day,  $N = 11$ ) than females in old-growth areas ( $1.5 \pm 0.36$  copulations/day,  $N = 11$ ). Furthermore, the majority (73%) of sexual behaviours in logged areas occurred when females were fully



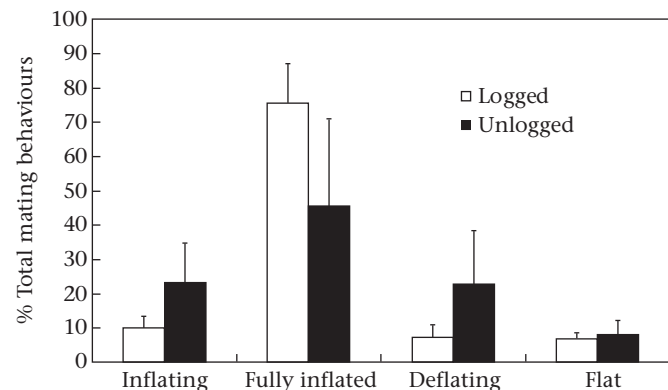
**Figure 2.** Copulation rates (number of copulations divided by the number of observation days, standardized by the number of adult males per group, and log transformed) of females living in logged and old-growth areas of Kibale National Park.

tumescent. In comparison, only 46% of sexual behaviours occurred during maximal swelling in old-growth areas ( $Z = -2.45$ ,  $P = 0.012$ ). However, mating behaviours during periods of deflating were higher for females in old-growth areas (mean  $\pm$  SD =  $22.85 \pm 15.58$ ) than for females in logged areas ( $7.41 \pm 3.61$ ;  $Z = 1.77$ ,  $N = 22$ ,  $P = 0.046$ ). Furthermore, there was a trend suggesting that females in old-growth areas had a higher percentage of mating behaviours ( $23.33 \pm 11.39$ ) than females in logged areas ( $10.05 \pm 3.32$ ) when genital swellings were inflating ( $Z = 1.62$ ,  $N = 22$ ,  $P = 0.060$ ). Females in logged and old-growth areas showed no difference in frequency of mating behaviours when flat (no tumescence) ( $Z = 0.82$ ,  $P = 0.212$ ; Fig. 3). Neither in logged areas nor in old-growth areas did females copulation calls, as has been documented in other populations of red colobus monkeys (Starin, 1991).

## DISCUSSION

This study provides evidence for plasticity in primate reproductive strategies in the face of ecological constraints. Female red colobus in logged areas had a shorter duration of maximal swelling than females in old-growth areas. Females in logged areas also copulated less frequently than females in old-growth areas and their mating was more constrained to the period of maximal tumescence. Females in old-growth areas tended to mate during periods of inflating and deflating more often than females in the logged areas and, thus, were less constrained than females in logged areas that limited their mating to maximal tumescence.

This pattern supports Wrangham's (2002) cost of sexual attraction hypothesis, in which females minimize their energy expenditure by reducing sexual attractivity and limiting copulation to conception periods. This strategy may be key to maintaining reproductive function in degraded habitats. Looking at individual females from each area helps to show how the general pattern fits with each subject. For example, a female in the logged area that gave birth in early April 2010 was seen copulating multiple times per day for several consecutive days in early November 2009 (approximately 5 months before the birth of her infant). Hormone analyses of faecal samples from this female showed a peak in oestradiol just before these days of frequent mating, followed by a sustained rise in progesterone. This period in late October/early November was also when she had a fully tumescent genital swelling. The female did not mate at any other point in her cycle while we were observing her, unlike a female from the old-growth area who was seen mating on several days throughout the cycle. This female from the old-growth area gave birth in late June 2010



**Figure 3.** Mating behaviours in relation to extent of perineal swelling in red colobus females living in logged and old-growth areas of Kibale National Park.

and had a fully tumescent genital swelling in late January, following a peak in oestradiol in mid-January. She mated on several days in late January while in her periovulatory phase, but she also was seen mating in early January and late November. Neither of these other mating bouts was during periods of increased oestradiol concentrations or fully tumescent genital swellings.

Wrangham's original hypothesis was more focused on the cost of grouping for a fission–fusion species; however, here we show that there are costs to sexual attraction aside from increasing subgroup size. Red colobus largely remain in cohesive groups, so variation in sexual behaviours and swelling durations are associated with other factors beyond increasing feeding competition. Females incur potential costs of mating, including injury, predation and contracting diseases (Daly, 1978; Hosken & Snook, 2005; Huchard et al., 2012; Rice & Holland, 1997; Small et al., 1988; Tregenza, Wedell, & Chapman, 2006; Warner, Shapiro, Marcanato, & Petersen, 1995). Some researchers suggest that mating may be associated with energetic costs both from increased energy expenditure and reduced feeding time (Daly, 1978; Small et al., 1988), and this may be particularly important for females in logged areas, which spend more time feeding than do females in old-growth forest. For example, Huchard et al. (2012) found that there were significant energetic costs associated with mating for female grey mouse lemurs, *Microcebus murinus*. As a result, females in better energetic condition had higher mating rates (Huchard et al., 2012). Even if reduced food availability in the logged area is not enough to cause energetic constraints, then added stress from increased parasite loads in disturbed areas certainly could (Chapman & Chapman, 1999; Gillespie & Chapman, 2001; Snaith, Chapman, Rothman, & Wasserman, 2008). Thus, female red colobus facing greater energetic constraints from living in a degraded habitat with lower food availability limit their mating activities.

Behavioural plasticity has been argued to be adaptive traits (West-Eberhard, 2003) that are particularly important when individuals are faced with changing environmental conditions (Pigliucci, 2001). By increasing the degree of phenotypic response to environmental cues (i.e. by increasing plasticity), populations may adapt to changing environments quickly and without necessitating genetic change. This increase in plasticity may, for example, allow individuals to cope with new energetic constraints in novel habitats in order to maintain a positive energy balance needed for reproductive function. These behavioural and physiological changes may be sufficient to maintain a positive energy balance and reproductive hormone concentrations needed for reproductive function.

Behavioural plasticity was originally conceptualized as a lack of specialization and was associated with generalists (Klopfer & MacArthur, 1960); however, growing evidence supports plasticity as a strategy for both specialists and generalists (Greenberg, 1990; Morse, 1980). Different primate species are often categorized as specialized for their environments; however, the occurrence of individual species across multiple habitat types and evidence for their behavioural plasticity suggests that primates have a tolerance for and an adaptive potential to live in various ecosystems (Jones, 2005; Strier, 2011) and respond to changing environments (Morse, 1980). Half of the primate species in the world are endangered, and most are facing drastic environmental changes; thus, it is important to understand the degree of plasticity that each species shows to ascertain their extinction risk. While many primate species have been thought to be specialists, increasing evidence shows that some primates may be more flexible than previously thought. Our own data show that red colobus are just such a case.

Increased phenotypic plasticity may allow females to maintain reproductive function in degraded habitats, but the patterns



observed in this study suggest that there may be other repercussions for female reproductive success in logged areas of Kibale. Reproduction is costly for female primates, where females invest considerable time and energy into successfully rearing offspring (Stumpf et al., 2011). Female use a variety of reproductive strategies to cope with both social and ecological challenges, including infanticide avoidance (Heistermann et al., 2001; Hrdy, 1979; van Noordwijk & van Schaik, 2000; Wolff & Macdonald, 2004), cryptic female choice (van Noordwijk & van Schaik, 2000; Wolff & Macdonald, 2004), indirect benefits, such as friendship (Palombit, 2009; Palombit et al., 2001), and combinations of each (Stumpf & Boesch, 2005). Females in old-growth areas that are less constrained by the cost of sexual attraction can use strategies for paternal confusion and infanticide avoidance more flexibly, including mating outside of periovulatory periods. However, under adverse ecological conditions, females may not have the energetic surplus necessary for a flexible mating strategy and may have to hedge their bets via more temporally constrained mating around periovulation. Long-term fitness consequences could result for females in degraded areas if ecological stressors constrain a female's ability to flexibly use these strategies.

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