



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 km²; 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).

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