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Management of Synanthropic Macaque (*Macaca fascicularis*) Populations in Bali: Assessing the Implications of Sterilization on Female Social Dynamics

Gwennan Giraud[1,2] · **I. Nengah Wandia**[3] · **Alain Hambuckers**[1] · **Fanny de Thier Nagelmackers**[1] · **Stefan Deleuze**[4] · **Marie‑Claude Huynen**[1] · **Fany Brotcorne**[1]

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Abstract

Growing contacts between humans and nonhuman primates at interface zones bring forth the need to better understand the efficiency and implications of synanthropic primates population management strategies. In this context, the expanding use of fertility control contrasts with the limited documentation of its potential consequences for primate behavior and social dynamics. Unlike other methods, tubectomy preserves the ovarian functions involved in sexual motivation of female macaques. However, sexual behaviors and aggression could intensify due to a higher proportion of cycling females within the group. In this study, we assessed whether tubectomy modifies the sociosexual interactions of female long-tailed macaques (*Macaca fascicularis*) in a primate-tourism site in Bali, Indonesia. Using focal sampling over a three-year period ($N = 56$ females), we investigated changes in (a) female sociosexual activities (i.e., sexual and grooming interactions with males), and (b) female intrasexual aggression (i.e., female-female agonistic interactions). Using causal inference statistics, we found that (a) compared with intact females, sterilized females were more sexually receptive and attractive, and they received longer grooming bouts from male partners. Surprisingly, (b) tubectomy was associated with decreased intrasexual aggression among females, as sterilized females received

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Badges earned for open practices: Open Data and Open Analytical Code. Experiment materials and data are available in the repository at https://github.com/GwennanGiraud/Implications-of-synanthropic-female-macaque-sterilization.

Extended author information available on the last page of the article

aggression from fewer female opponents compared with intact females. This study showed that, at least in the short term, tubectomy modifies the sociosexual interactions, while not heightening female aggression. These findings may inform management decisions that maximize social stability and welfare of synanthropic populations. However, the long-term implications of female sterility for social dynamics warrant further investigation.

Keywords Fertility control · Long-tailed macaques · Causal inference · Female competition · Mating market · Tubectomy

Abbreviations

IUCN	International Union for Conservation of Nature
SSC	Species Survival Commission
SSR	Socionomic Sex Ratio

Introduction

Among the major global changes of the Anthropocene, land-use modification has increased proximity between humans and wildlife (König *et al.*, 2020), leading to diverse interspecific interactions in shared habitats (Torres et al., 2018). These interactions can be challenging when human and wildlife needs overlap, particularly when wildlife presence results in economic losses for local communities, such as crop damage or livestock predation (IUCN Species Survival Commission (SSC) 2023; White & Ward, 2010). Opportunistic and highly adaptive species, such as macaques or baboons, are particularly prone to such situations. Their opportunistic and generalist ecology allows them to thrive in anthropogenic environments (Choong *et al.*, 2021; Hockings, 2016; Sol *et al.*, 2013). These dynamics may harm both humans and wildlife, sometimes even driving local extinctions with cascading effects on ecosystems (Ripple *et al.*, 2014). Promoting human-wildlife coexistence therefore requires multidisciplinary strategies involving communities, stakeholders, and scientists (Dickman, 2010; IUCN SSC, 2023). Negative interactions with humans are particularly frequent in areas of high local densities within restricted anthropogenic habitats (Brotcorne *et al.*, 2011; Choong *et al.*, 2021), underscoring the need for sustainable and well-informed management approaches.

Managers increasingly use fertility control via surgical sterilization or hormonal contraception to regulate the size of free-ranging primate populations perceived as locally "overabundant." Fertility control is becoming a more popular alternative to culling and translocation (Mikail *et al.*, 2023). Yet, sociobehavioral changes associated with fertility control remain poorly documented, especially in free-ranging primates. Controlling fertility in social animals requires surgical sterilization techniques, such as vasectomy and tubectomy (Phoenix, 1973; Yu *et al.*, 2015). These methods avoid hormonal disruption and are appropriate for wild primates, including macaques (Deleuze *et al.*, 2021; Kumar & Raj, 2013; Zhao *et al.*, 1984). Given the role of sex steroid hormones in sexual motivation and sociosexual behaviors of simian primates (Beach, 1976; Dixson, 2012; Michael & Zumpe, 1993; Wallen, 2001), sterilization by tubectomy should maintain female individuals' motivation for mating and their investment in socio-reproductive activities, such as grooming exchanges with males after copulation (Gumert, 2007) or increased agonistic behaviors among females during their follicular phase (Mallow, 1981). For instance, in long-tailed macaques (*Macaca fascicularis*), tubectomized females keep interacting with males when mating opportunities occur (Giraud *et al.*, 2021). However, repeated nonconceptive cycles disrupt life-history traits, as the females in this species normally conceive after one or two fertile cycles (van Noordwijk, 1985).

Measuring the behavioral implications of fertility control at the individual and group levels requires an investigation of sociosexual dynamics. Sociosexual interactions, including copulations, grooming, and agonistic interactions, allow us to measure partner choice and intrasexual competition. Foundational theory (Beach, 1976) classified female primate sexual behaviors into three distinct categories: proceptivity, receptivity, and attractivity. Female proceptivity, which serves as a proxy of female sexual motivation, translates into behavioral patterns displayed by females to initiate and maintain sexual interactions with males. Female attractivity, assessed through male-initiated behaviors, refers to a female's morphological or behavioral cues that increase the likelihood of eliciting sexual appetitive reactions of a male. Finally, female receptivity, often defined as the consummatory phase of mating, refers to the willingness of females to accept the males and allow copulation with intravaginal ejaculation. Primates use grooming behavior as another important component of sexual interactions (Dixson, 2012; Gumert, 2007; Sonnweber *et al.*, 2015). For example, macaques typically exchange grooming and sexual contacts (Gumert, 2007), and the frequency and patterns of these exchanges shift across female reproductive conditions. The phases in the ovarian cycle of rhesus macaques (*M. mulatta*) influence grooming dynamics between males and females (Michael *et al.*, 1966). In Barbary macaques (*M. sylvanus*), lactating females initiate grooming with males more frequently than males do with them after copulation, whereas nonlactating females do not show such a difference in postcopulation grooming initiations (Sonnweber *et al.*, 2015). These variations may reflect hormonal changes associated with female reproductive condition (Dixson, 2012; Wallen & Zehr, 2004). However, sexual interactions also serve social functions beyond reproduction, such as reinforcing social bonds or maintaining hierarchical positions, potentially further amplifying competition among females (Gumert, 2010; Gumert & Ho, 2008; Sonnweber *et al.*, 2015; Thierry, 2007).

Male-male competition and female mate choice were first highlighted in the context of sexual selection and variation in mating success (Bateman, 1948; Darwin, 1871). Conversely, female intrasexual competition and male mate choice have received less attention (Rosvall, 2011; Stockley & Bro-Jørgensen, 2011; Tang-Martinez, 2016). A relatively recent shift in the field has underscored the need to reconsider the conventional Bateman's paradigm of sex differences, which portrays the male as combative and promiscuous, and the female as passive and highly selective (Drea, 2005). Females play an active role in access to males through varied tactics, sometimes cryptic, they employ to improve their reproductive success and social integration (Cheney *et al.*, 2012; Gumert, 2007; Wasser & Barash, 1983). While female competition over mates may be less overt than male-male competition

(Tang-Martinez, 2016), it can nonetheless have significant social and reproductive consequences, especially in species with complex social organization (Huchard & Cowlishaw, 2011). Biological Market Theory posits that the supply and demand of services, such as sex and grooming, influence partner choice (Noë & Hammerstein, 1994). Given the functional significance of grooming in primates (Dunbar, 1991), competition for grooming partners may be meaningful in this realm (Hemelrijk & Luteijn, 1998; Seyfarth, 1977). In contrast to female-male grooming, which normally increases in the context of sexual interactions, female-female grooming varies inversely with sexual activity, decreasing significantly during the mating period and fertile phase, while female-female agonistic interactions increase (Mallow, 1981; Wallen & Tannenbaum, 1997; Xia *et al.*, 2012). However, Wallen & Tannenbaum (1997) suggest that the increase in aggression may be a response to disruptions in the group's social structure.

Besides the relative role of sex hormones in regulating sexual motivation, the sex ratio within a group influences the sexual interest of both males and females toward potential partners (Wallen, 2001). In multimale/multifemale cercopithecine societies, philopatric females represent the social core of the group, and females generally outnumber males in the adult sex ratio (Thierry, 2000). However, mating seasonality influences the operational sex ratio (i.e., the number of fertilizable females per sexually active male at a given time) in some species, which in turn influence the level of intrasexual competition (Emlen & Oring, 1977; Hemelrijk & Luteijn, 1998; Kvarnemo & Ahnesjo, 1996; Thierry, 2000). Typically, an imbalanced operational sex ratio promotes sexual competition through monopolization of partners, reproductive suppression, or direct contest competition among members of the most abundant sex (Cheney *et al.*, 2012; Huchard & Cowlishaw, 2011). Because sterilization typically modifies the operational sex ratio of a primate group, it may affect social dynamics.

The long-tailed macaque is a well-suited species to investigate the effects of sterilization on social dynamics. As a synanthropic primate, it frequently lives in close association with humans and can benefit from anthropogenic resources, such as rice shoots from agricultural plantations (Gumert *et al.*, 2011; Klegarth, 2017). The species occurs widely across South-East Asia (IUCN, 2024), yet it is increasingly threatened by habitat loss, trade demand, and removal associated with human-macaque interactions, leading to marked global declines (Gamalo *et al.*, 2024; Hansen *et al.*, 2022; IUCN SSC, 2023). Therefore, although some populations have become highly visible in anthropogenic landscapes owing to habitat loss, others are paradoxically becoming less abundant or disappearing (Eudey, 2008; Holzner *et al.*, 2025; Kabir & Ahsan, 2012). In many areas, the species persists at unusually high local densities within restricted anthropogenic habitats (Brotcorne *et al.*, 2011; Choong *et al.*, 2021), raising pressing questions about its management and the consequences of interventions such as sterilization.

In the Ubud Monkey Forest, Bali (Indonesia), a fertility control program uses tubectomy as a means to manage the growth of the long-tailed macaque population (Deleuze *et al.*, 2021). The rationale behind this program arises from the need to regulate, at a local scale, the unusually high macaque density within a confined area. This abundance appears linked to escalating social tensions both among macaques and between macaques and humans (Brotcorne *et al.*, 2023). Social network analysis of this population showed that sterilized females' centrality—estimated from female-female affiliative networks shortly after sterilization—did not differ from those of intact females (Giraud *et al.*, 2021). However, it remains unclear whether prolonged reproduction suppression in sterilized females alters their sociosexual interaction patterns. If tubectomized females remain sexually motivated and available for mating, this could alter female-female competition dynamics. Therefore, we investigated the effects of tubectomy-induced sterilization on two groups of long-tailed macaques, focusing on potential changes in 1) female sociosexual activities (i.e., sexual and grooming interactions with males), and 2) female intrasexual aggression (i.e., female-female agonistic interactions). Unlike intact females, tubectomized females could experience repeated nonconceptive cycles and could remain sexually active due to the absence of gestation and lactational constraints. We hypothesized that this would lead sterilized females to invest more in sociosexual interactions with males, including solicitations and grooming. Accordingly, we predicted that, compared with intact females, sterilized females would increase their sexual interactions with males, reflected by greater proceptivity, attractivity, and receptivity, as well as engage in longer grooming bouts and with more male partners. We also hypothesized that the prolonged and uneven distribution of sexual receptivity, along with grooming-related dynamics with males, disrupts the group's social structure (Wallen & Tannenbaum, 1997), predicting an increase in female-female agonistic interactions.

Methods

Study Site and Study Groups

The Ubud Monkey Forest lies in central Bali, Indonesia (8°31′ S, 155°15′ E). This 20-ha forest sanctuary shelters wild long-tailed macaques who have coexisted with people for a long time (Wheatley, 1999). The macaque tourism hotspot has benefitted the local human community for decades (Howells *et al.*, 2022). They manage the site and provision the macaques with fruits and vegetables to keep them in the forest (Fuentes, 2010). The regular access to food and the weak predation pressure have likely contributed to the expansion of the macaque population, with a mean annual growth rate of 10% over 30 years (Brotcorne *et al.*, 2015). In June 2017, the macaque population density reached 37 individuals per hectare, with 749 individuals in six groups.

Between 2017 and 2019, managers and researchers collaborated on four sterilization campaigns (July 2017, July 2018, February 2019, and August 2019), using endoscopic tubectomy to sterilize 136 females in the population (Deleuze *et al.*, 2021). In parallel, we monitored the macaques' behavior to assess potential side effects of reproduction suppression. We focused this behavioral study on two groups, "Michelin" (mother group) and "Utara" (daughter group), which were a single group until the end of 2018 (Table 1). Identified adult individuals represented a mean of 86 % (± SD 42) of the entire adult group sizes. Over the 3 years, the staff sterilized 16

Table 1 Demographic composition of two study groups of long-tailed macaques in Ubud Monkey Forest (Indonesia) between 2018 and 2020, and maximum number of identified individuals per year. Michelin and Utara were one group in 2018 before their fission. SSR = socioeconomic sex ratio

Group	Category	2018	2019	2020
Michelin	Adult males	15–16	16–21	12–17
	Adult females	50–54	43–47	50–57
	Total adults	65–70	59–68	62–74
	Sterilized females	*1–3*	*2–15*	*12–13*
	SSR	*2.1*	*1.6*	*1.8*
Utara	Adult males	NA	4–6	7
	Adult females	NA	7–9	10
	Total adults	NA	11–15	17
	Sterilized females	NA	*1*	*1*
	SSR	NA	*1.8*	*1.1*
Maximum number of identified individuals		***68***	***67***	***61***

females in the Michelin group, and one female in the Utara group (*N* = 17 sterilized females). Annual demographic censuses of the groups (Giraud *et al.*, 2021) showed that the socionomic sex ratio (SSR, i.e., the ratio of sexually mature (subadult and adult) females to sexually mature males) was slightly biased toward females (range: 1.1–2.1) over the three study years in both groups (Table 1).

Data Collection

One observer collected most of the data over 25 months from 2018 to 2020 (Jan. to Sep. 2018; Jan. to Aug. 2019; Dec. 2019 to Mar. 2020; and Sep. to Nov. 2020). Another observer contributed to data collection in July to September 2019. The interobserver reliability (calculated as the mean Spearman correlation coefficient for behavior durations, *N* = 21 focal samples) was 86% (Martin & Bateson, 1993). Using the Animal Behaviour Pro V.1.2. app (Newton-Fisher 2012), we used 15-min focal sampling (Altmann, 1974) to collect behavioral data on 56 focal females (49 females in Michelin and 7 females in Utara; Supplementary Information S1). Observations covered a total of 178.5 h of focal data in 2018 (mean = 3.4 ± 0.2 h/female), 218.2 h in 2019 (mean = 4.3 ± 0.2 h/female), and 338.5 h in 2020 (mean = 7.1 ± 0.2 h/female). For sociosexual interactions, we noted the identity of each interactor of the focal individual (when possible) and the direction of the interaction (i.e., focal individual being giver versus receiver). We recorded sexual interactions with males, and agonistic and grooming interactions with females and males (ethogram in Supplementary Information S2).

Ethical Note

The Indonesian Ministry of Research and Technology approved the research protocol of this study (SIP Research permits: No. 419/SIP/FRP/E5/Dit.KI/XI/2017; No. 39/EXT/SIP/FRP/E5/Dit.KI/VII/2018; No. 53/E5/E5.4/SIP.EXT/2019). We conducted the research to complement a birth control program, whose objectives and protocol received approval from the Indonesian Ministry of Research and Technology (SIP Research permits: No. 46/SIP/FRP/E5/Dit.KI/II/2018, No. 10/E5/E5.4/SIP.EXT/2019, No. 83/E5/E5.4/SIP.EXT/2019), the Animal Ethics Commission of Udayana University (No. 282/KE-PH/I/2017), and the Provincial Office of Conservation in Bali (BKSDA, No. S.538/BKSDA.BL-1/KK/7/2019; Capture license: #29/PPSP/XII/2017). This study was purely observational and complied with the International Primatological Society Code of Best Practices for Field Primatology. The authors declare that they have no conflict of interest.

Data Availability The datasets analyzed and R script used during the current study are available in the Github Repository: https://github.com/GwennanGiraud/Implications-of-synanthropic-female-macaque-sterilization.

Statistical Analysis

To investigate the consequences of female reproduction suppression on social dynamics, we used a causal inference method called the “Fisher’s exact *P*-values for completely randomized experiments” (Imbens & Rubin, 2015). This approach enabled us to compare intact and tubectomized females before versus after sterilization, accounting for the four different sterilization dates across the successive campaigns between 2018 and 2020 (Supplementary Information S1). To ensure comparability, we assigned intact females a random pseudo-date of sterilization, allowing us to analyze their behavior across two analogous periods as for sterilized females (“before” vs. “after”), and therefore serve as a control group. The analysis relies on both within-subject and between-subject comparisons across the two periods.

The causal inference method offers key advantages over classical multivariate regression models. First, it provides robust evidence of a causal relationship between the response variable (here, the social behavior of interest) and the predictor (here, the tubectomy treatment). Second, is that it does not rely on assumptions about the distribution of the dependent variable, making it robust against potential statistical biases (Imbens & Rubin, 2015).

As response variables, we analyzed

1) The occurrences of sexual interactions, which we categorized as proceptivity, attractivity, or receptivity;
2) The durations of grooming bouts given and received; and
3) The occurrence of agonistic interactions given and received.

For each of these three behaviors of interest, we tested two parameters:

1) The total observed values (i.e., occurrences or durations), and
2) The total number of social partners.

To control for unbalanced sampling effort between individuals and between periods and ensure comparability across individuals and timeframes we normalized the two parameters by dividing them by the total focal observation effort (hours) for each period.

We computed two test statistics (T_1 & T_2) for each response variable. T_1 estimates the treatment effect. In our case, it quantifies the effect of sterilization by comparing mean posttreatment behavior between sterilized and intact females (i.e., between-subject comparisons). Including pseudo-treatment dates for intact females, we repeatedly computed the same statistic ($T0_1$) under the null hypothesis by randomizing treatment assignments ($N = 1{,}000$). The significance of T_1 is the probability of observing a treatment effect under the null hypothesis. We computed this significance as the fraction of $T0_1$ statistics that equal or exceed T_1. Given that sterilization date varied across individuals (Supplementary information S1), we also randomized the date of treatment when computing mean behaviors to derive the $T0_1$ vectors.

T_2 compares the differences in mean behaviors of sterilized females after and before treatment (i.e., within-subject differences) with those of intact females (i.e., between-subject comparisons). For instance, if sterilized females spent a mean of 20 minutes per hour grooming after treatment, compared with 10 min per hour before treatment, while intact females showed no change (e.g., 15 min per hour both before and after), T_2 would assess whether the observed increase in grooming among sterilized females is significantly greater than any natural fluctuation seen in intact females. Unlike classical regression models, T_2 test has the advantage of implicitly accounting for potential co-factors explaining initial differences in sociality between the females such as their life-history traits, dominance rank and age (Liao *et al.*, 2018; Seyfarth, 1977). This approach is particularly suitable given our limited sample size (17 sterilized females out of 56 total females), as traditional regression models would require extensive covariate control to robustly isolate the treatment effect (Zuur *et al.*, 2009).

We performed all analyses using R 4.0.3 software (R Development Core Team 2013).

Results

Effects of Sterilization on Sociosexual Activities

Proceptivity

Sterilized females did not significantly differ from intact females in frequencies of proceptive behaviors, nor in the number of males they solicited (Table 2). Sterilization therefore appeared to have no significant impact on sexual motivation.

Attractivity

Intact and sterilized females did not receive significantly different sexual interest from males (Table 2). However, sterilized females became significantly more

Table 2 Causal effects of sterilization treatment on sexual behavior frequencies and on numbers of male sexual partners per hour in female long-tailed macaques at Ubud Monkey Forest (Indonesia, January 2018 to November 2020). Significant values are in bold. After = behavior after sterilization (virtual for intact females); Before = behavior before sterilization

	Proceptivity		Attractivity		Receptivity	
	Frequency (events per hour)	Partner number per hour	Frequency (events per hour)	Partner number per hour	Frequency (events per hour)	Partner number per hour
T_1: Comparison between sterilized and intact females after sterilization						
Mean intact After	0.18	0.41	0.18	0.44	0.17	0.21
Mean sterilized After	0.26	0.53	0.24	0.64	0.45	0.46
T_1	0.11	0.12	0.10	0.20	0.16	0.26
Mean T_1	0.06	0.08	0.04	0.09	0.06	0.06
Standard deviation T_1	0.04	0.06	0.03	0.07	0.04	0.05
***P*-value T_1**	0.12	0.24	0.07	0.09	**0.02**	0.56
T_2: Comparisons of "after-before" treatment differences between sterilized and intact females						
Mean intact After - Before	0.12	0.10	0.11	0.11	0.09	0.004
Mean sterilized After - Before	0.21	0.24	0.20	0.18	0.43	0.24
T_2	0.14	0.13	0.14	0.08	0.23	0.24
Mean T_2	0.06	0.12	0.05	0.17	0.07	0.10
Standard deviation T_2	0.04	0.09	0.04	0.13	0.05	0.08
***P*-value T_2**	0.07	0.42	**0.049**	0.74	0.08	0.09

attractive after treatment, whereas intact females showed stable levels of attractivity across the same time frame. Although intact females also became more attractive over time, sterilized females showed a significantly greater increase in attractivity (Fig. 1a). Thus, sterilized females became more attractive to males than intact females. In contrast, intact and sterilized females did not differ in the number of male partners attracted to them (Fig. 1b).

Receptivity

After treatment, sterilized females displayed significantly more receptive behaviors than intact females (Table 2; Fig. 2a). However, both sterilized and intact females showed an increase in receptive behaviors across the same time frame. This increase did not differ significantly between both female categories. Sterilized and intact females also did not differ significantly in the number of males they copulated with (Fig. 2b).

Grooming with Males

During the post-sterilization period, sterilized females were groomed for significantly longer than intact females (Table 3; Fig. 3a) and by more male partners (Fig. 3b). Although males increased grooming with both female categories after

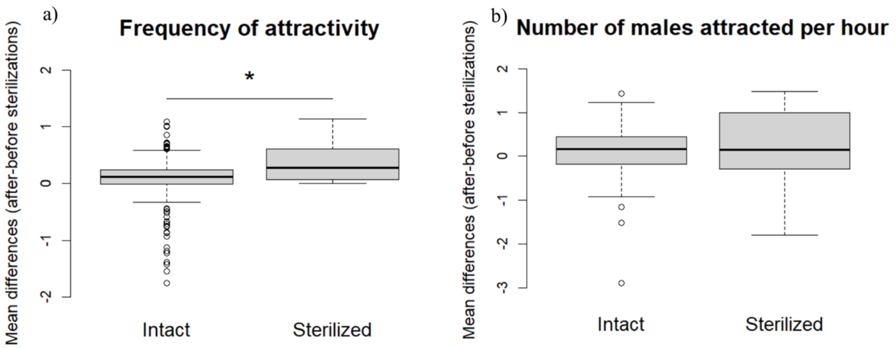

Fig. 1 Mean differences (after – before treatment) in female attractivity for sterilized and intact female long-tailed macaques at Ubud Monkey Forest (Indonesia, January 2018 to November 2020). (**a**) Frequency of attractivity behaviors (occurrences/hour). (**b**) Number of male partners per hour. Boxes = interquartile range, line = median, whiskers = full range, points = individual females. We randomly assigned pre- and post-"treatment" periods for intact females. *$P < 0.05$.

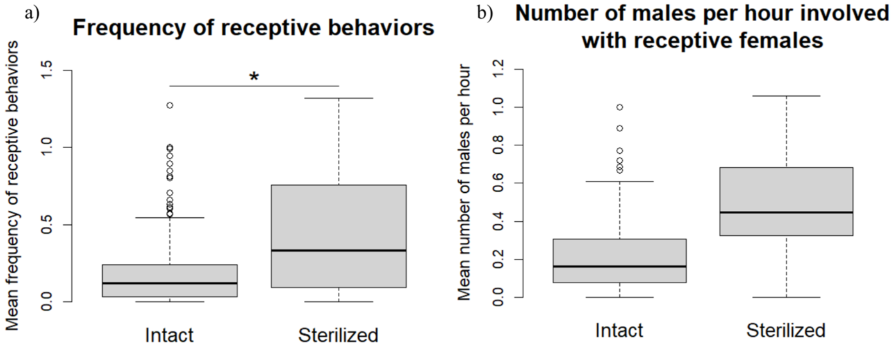

Fig. 2 Mean differences in female receptivity after sterilization between intact and sterilized female long-tailed macaques at Ubud Monkey Forest (Indonesia, January 2018 to November 2020). (**a**) Frequency of receptive behaviors (occurrences/hour). (**b**) Number of male partners per hour. Boxes = interquartile range, line = median, whiskers = full range, points = individual females. We randomly assigned pre- and post-"treatment" periods for intact females. *$P < 0.05$.

treatment compared with before, the increase was significantly greater for sterilized females. We also found an increase in the number of male partners grooming both categories of females after treatment, with a greater increase in sterilized females; but this difference was not statistically significant ($P = 0.06$). Conversely, females did not differ significantly in the duration with which they groomed males, or in the number of males they groomed.

Effects of Sterilization on Female-Female Agonistic Interactions

Contrary to our prediction that female-female agonistic interactions would increase after sterilization, sterilized females and intact females showed no significant

Table 3 Causal effects of sterilization treatment on grooming duration with males and on numbers of male partners per hour in female long-tailed macaques at Ubud Monkey Forest (Indonesia, January 2018 to November 2020). Significant values are in bold. After = behavior after sterilization (virtual for intact females); Before = behavior before sterilization

	Duration ♀ Receptor	Partner number per hour	Duration ♀ Emitter	Partner number per hour
T_1: Comparison between sterilized and intact females after sterilization				
Mean intact After	1.52	0.18	2.56	0.27
Mean sterilized After	4.19	0.40	4.25	0.41
T_1	1.60	0.21	0.65	0.14
Mean T_1	0.61	0.07	0.71	0.07
Standard deviation T_1	0.45	0.05	0.53	0.05
***P*-value T_1**	**0.03**	**0.04**	0.49	0.09
T_2: Comparisons of "after-before" treatment differences between sterilized and intact females				
Mean intact After - Before	1.00	0.05	1.48	−0.01
Mean sterilized After - Before	3.93	0.26	3.79	0.11
T_2	1.86	0.22	1.19	0.12
Mean T_2	0.70	0.08	0.82	0.11
Standard deviation T_2	0.52	0.06	0.60	0.08
***P*-value T_2**	**0.04**	0.06	0.26	0.42

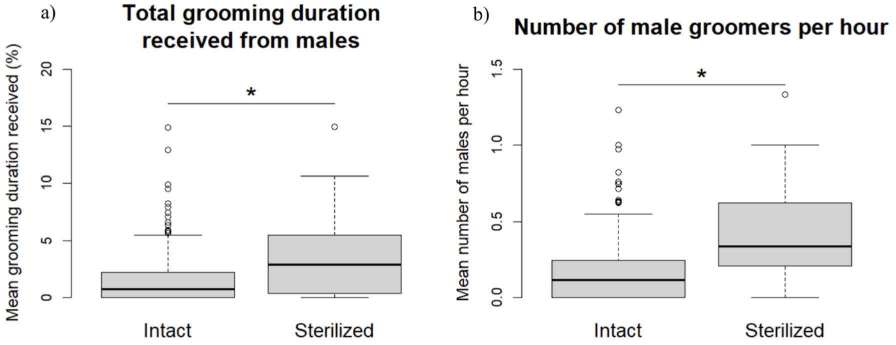

Fig. 3 Mean differences in female-male grooming after sterilization between intact and sterilized female long-tailed macaques at Ubud Monkey Forest (Indonesia, January 2018 to November 2020). (**a**) Percentage of grooming duration received from males. (**b**) Number of male groomers per hour. Boxes = interquartile range, line = median, whiskers = full range, points = individual females. We randomly assigned pre- and post-"treatment" periods for intact females. *$P < 0.05$.

difference in how often they were agonistic toward other females or how often they received agonism from other females (Table 4; Fig. 4a). They also did not differ in the number of female opponents they were aggressive to. Therefore, we found no evidence that female-female aggression increased after sterilization. However, fewer female opponents aggressed sterilized females than intact females (Fig. 4b).

Table 4 Causal effects of sterilization treatment on female-female agonistic behavior frequencies and on numbers of female opponents per hour in female long-tailed macaques at Ubud Monkey Forest (Indonesia, January 2018 to November 2020). Significant values are in bold. After = behavior after sterilization (virtual for intact females); Before = behavior before sterilization

	Frequency (events per hour): Receptor	Opponent number per hour	Frequency (events per hour): Emitter	Opponent number per hour
T_1: Comparison between sterilized and intact females after sterilization				
Mean intact After	0.63	1.07	0.42	0.75
Mean sterilized After	0.72	1.05	0.35	0.72
T_1	0.092	0.04	0.02	0.04
Mean T_1	0.12	0.17	0.09	0.15
Standard deviation T_1	0.089	0.12	0.07	0.11
***P*-value T_1**	0.55	0.85	0.89	0.84
T_2: Comparisons of "after-before" treatment differences between sterilized and intact females				
Mean intact After - Before	0.34	0.03	0.25	0.02
Mean sterilized After - Before	0.53	−0.79	0.26	−0.22
T_2	0.08	0.82	0.09	0.25
Mean T_2	0.16	0.30	0.10	0.24
Standard deviation T_2	0.12	0.21	0.08	0.17
***P*-value T_2**	0.72	**0.02**	0.54	0.43

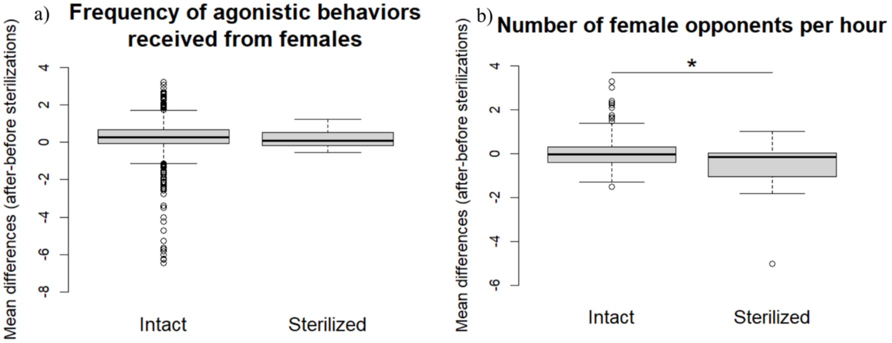

Fig. 4 Mean differences (after – before treatment) in female-female agonistic interactions for sterilized and intact female long-tailed macaques at Ubud Monkey Forest (Indonesia, January 2018 to November 2020). (**a**) Frequency of agonistic behaviors received (occurrences/hour). (**b**) Number of aggressors per hour. Boxes = interquartile range, line = median, whiskers = full range, points = individual females. For intact females, pre- and post-"treatment" periods were randomly assigned. *$P < 0.05$.

Discussion

In our 3-year behavioral monitoring of Balinese long-tailed macaques, we found that tubectomy increased sociosexual activities of sterilized females with males. As a result, sterilized females were more sexually active, specifically more receptive and attractive to males, but not more proceptive, than intact females. Contrary to our prediction, this situation did not intensify female-female aggression. Instead, we observed some indications of reduced intrasexual aggression for sterilized females.

Tubectomy Increases Female Sociosexual Activities

As predicted, we found that tubectomy preserved the sociosexual activities of treated females, and even intensified the frequency of some sexual behaviors. Overall, this is consistent with the role of sex steroid hormones—primarily progestogen and estrogen, which remain intact after tubectomy—in maintaining behaviors and sexual motivation (Beach, 1976; Dixson, 2012). Although simian primates are relatively emancipated from a strict hormonal control in their physical ability to copulate compared with other mammalian species, sex hormones influence various aspects of sociality, including the establishment of social status (Michael & Zumpe, 1993; Richards *et al.*, 2009), sexual activity, and stress coping mechanisms (Létang *et al.*, 2021; Wallace *et al.*, 2016; Wallen & Zehr, 2004). Specifically, we found that tubectomized females were more receptive to males than intact females after sterilization campaigns. However, both sterilized and intact females showed an increase in receptive behaviors across the same time frame. Therefore, this difference might not be solely due to the presence or absence of treatment. Nevertheless, previous earlier social network analysis suggested that sterilized females may attempt to stay in the vicinity of central males in the network (Giraud *et al.*, 2021). Combined with our observation that tubectomized females received more grooming from males, our results are consistent with those of a previous study showing that males invest in longer grooming bouts when females are sexually receptive (Gumert, 2007). Although males increased grooming efforts toward both categories of females across periods, the increase was higher for sterilized females. Sterilized females might therefore multiply consortships, i.e., copulations and grooming bouts with specific males, as an active strategy linked to female reproductive control (Drea, 2005). Male long-tailed macaques attempt to monopolize receptive females (Engelhardt *et al.*, 2006), which could explain the higher sexual attractiveness of sterilized females observed in our study. Longer-term monitoring of the treated females could confirm whether they consistently maintain a higher receptivity and attractivity toward males compared with intact females. Finally, the frequency of proceptive behaviors was similar between sterilized and intact females. Display of sexual motivation in female primates is species-specific. Long-tailed female macaques are highly permissive in their sexual contacts with males and express low levels of mate choice, displaying few behaviors of sexual solicitation (Engelhardt *et al.*, 2006). This likely explains why sterilization did not impact proceptive behaviors, used here as a proxy for female sexual motivation. Accumulating further data over a longer period of time could confirm this result.

Our results indicate that tubectomy preserves and even enhances socio-sexual interactions between treated females and males, despite the absence of significant changes in proceptivity. Other neutering methods, particularly hormonal contraceptives, cause behavioral modifications that contrast with these findings. For instance, treatment with Depo-Provera reduced female sexual attractivity while increasing agonistic behaviors in stumptail macaques (*Macaca arctoides*) (Linn & Steklis, 1990; Steklis *et al.*, 1982). Similarly, progestin-based contraception suppresses heterosexual behaviors in Japanese macaques (*M. fuscata*), including proceptivity, attractivity, and receptivity (Leca *et al.*, 2018). Finally, Ovral® (Wyeth Ayerst Laboratories, Philadelphia, PA; norgestrel, 0.5 rag; ethinyl estradiol, 50 ~g) treatment in dominant female long-tailed macaques led to a decline in the frequency of mounts involving intromission and ejaculation (Shively *et al.*, 1990). Reversibility and minimal invasiveness are important assets of temporary fertility control methods, such as hormonal contraception in captivity (Asa, 2016). However, these methods may still affect social stability. Moreover, the practical application of nonpermanent contraceptive methods poses significant challenges for free-ranging primate populations. Managers must carefully evaluate permanent neutering methods that neutralize sex hormones, such as gonadectomy, on welfare grounds, given the role of gonadal hormones in sociality, stress resilience, and coping mechanisms (Coleman *et al.*, 2011). They should also consider the welfare implications of fertility control methods for primates when developing management plans (Beausoleil & Mellor, 2015).

Tubectomy Does Not Increase Female Intrasexual Aggression

During the cycling period, particularly around the fertile phase, receptive macaque females typically exhibit heightened intrasexual aggression (Mallow 1981; Wallen & Tannenbaum, 1997). In our study, the increased sexual attractivity and receptivity of tubectomized females to males likely altered the operational sex ratio in the groups. As treated females remained cycling and available to males for extended periods, sterilization effectively increased the number of females available for mating per male than usual in this nonseasonal breeder (Brotcorne, 2014). As a result, we predicted an increase in intrasexual aggression among females and in male-female grooming interactions owing to disruption of the group's social structure through an increase in females available for mating (Cheney *et al.*, 2012; Huchard & Cowlishaw, 2011; Wallen & Tannenbaum, 1997). A recent long-term analysis of rhesus macaques in Cayo Santiago revealed that, although sex ratio does not predict female-female physical aggressions resulting in injuries, noncontact aggression increased in more female-biased groups (Pavez-Fox *et al.*, 2024). However, our findings did not support our prediction. Instead, aggression appeared to decrease after sterilization, as sterilized females received aggression from fewer female opponents than intact females. Despite the increase in the proportion of sterilized females in the mating market following successive sterilization campaigns, the relatively balanced socionomic sex ratio in our study groups (i.e., a high number of available males, ranging from 1.1 to 2.1 females per male) may have contributed to maintaining low levels of female intrasexual aggression in this nonseasonal breeder (Emlen & Oring, 1977; Thierry, 2000). For comparison, in other long-tailed macaque populations, the socionomic sex ratio varies considerably, ranging from 1.07 to 15 females per male in synanthropic populations in Bali and Singapore (Angst, 1975; Lute *et al.*, 2014).

Several aspects of female intrasexual competition remain unexplored in our study. Given the fitness-related costs of physical aggressions, especially in large groups, female macaques could further rely on indirect strategies to compete for resources (Pavez-Fox *et al.*, 2024). Competition can take the form of scramble competition by resource depletion (Janson & van Schaik, 1988; van Schaik & van Noordwijk, 1988) and is applicable to mating contexts (Kappeler, 1997; Radespiel *et al.*, 2001). In addition to agonistic competition females may also employ subtle reproductive strategies to outcompete rivals (Noë & Hammerstein, 1995). Instead of engaging in overtly aggressive interactions, they may use more subtle forms of rivalry, such as increased sociosexual engagement with males (Cheney *et al.*, 2012; Fisher & Krems, 2022; Tang-Martinez, 2016; Wallen & Tannenbaum, 1997). In the context of our study, we hypothesize that sterilized females monopolize male attention through increased grooming and sexual interactions, potentially limiting the strength of other female-male social bonds (Gumert, 2007; Wasser, 1983). Similarly, it would be relevant to investigate whether female-female grooming varies inversely with female sexual activity in our population, as reported in other studies (Wallen & Tannenbaum, 1997; Xia *et al.*, 2012). Our findings offer a first step in supporting the hypothesis that sterilized females engage in subtle sociosexual strategies, such as monopolizing males through grooming and displaying cues of sexual availability (increased receptivity), as active tactics to enhance their reproductive outcome (Drea, 2005).

This study has several limitations. Dominance rank skews reproductive success and influence mating strategies in female macaques (van Noordwijk & van Schaik, 1999). We did not assess the extent to which cofactors, such as rank, affect sterilized individuals. Testing such effects would require a different analytical framework, such as regression modelling, which would address a more fine-grained question than the one initially posed and a larger sample size. The strength of the design-based causal inference approach by Imbens & Rubin (2015) lies in its ability to control for confounding individual traits through both within-subject and between-subject comparison design. However, we verified that sterilized females were not concentrated in a single dominance rank category (Supplementary Information S3). Additionally, the limited number of sterilized females (17 vs. 40 intact females) is a clear constraint in our study, and the imbalanced sample may introduce a bias that reduces the generalizability of our findings. We should therefore exercise caution when extrapolating our results to the population-level. Future research should include larger and more balanced samples of sterilized and intact females to strengthen the validity of inferences and enhance the robustness of conclusions. Additionally, the number of sterilized females may have been too small to substantially alter the operational sex ratio within groups. Finally, the modified operational sex ratio following sterilization and the resulting behavioral changes in sterilized females are also likely to affect male-male competition, a key question currently under investigation (Giraud *et al.*, 2023).

Further studies should investigate whether sterilization affects individuals differently depending on their rank, or whether it can alter female dominance hierarchies in the long term. Given the long-life cycle of the study species (Fooden, 1995), we advocate collecting data over a longer period after sterilization. We call for studies assessing the implications of fertility control programs to better inform wildlife management protocols with a focus on animal welfare. Finally, while we focused on behavioral outcomes, future work should also consider the physiological implications of tubectomy and its potential long-term repercussions on health (Wallace *et al.*, 2016).

Conclusion

Our results show that tubectomy modified the sexual activities of female long-tailed macaques but did not increase sexual aggression among females in this population. These findings underline that fertility control can have behavioral consequences beyond reproduction itself, which is directly relevant to conservation, animal welfare, and fostering human-primate coexistence in shared habitats. Understanding such effects is essential for refining the development of welfare-oriented management strategies for synanthropic populations. We did not evaluate the effectiveness of sterilization in controlling population size, or address its potential role in mitigating human-primate conflicts. Current evidence linking sterilization to conflict mitigation remains limited (Shek, 2011). Importantly, population size does not always drive human-primate conflicts; even small primate populations can create conflict when their home ranges substantially overlap with human settlements (Jones-Engel *et al.*, 2011). While fertility control can contribute to regulate population growth when effectively implemented, it is often insufficient to reduce or resolve conflictual issues with human communities evolving with their own dynamics (Massei & Cowan, 2014). Achieving sustainable human-primate coexistence requires a holistic approach that integrates animal-focused measures (e.g., managing high population densities), environmental strategies (e.g., landscape management, food waste control), and human-focused actions (e.g., restricting provisioning, public awareness, and outreach initiatives) (Hockings, 2016; Jones-Engel *et al.*, 2011).

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Data Availability The datasets analyzed and R script used during the current study are available in the Github Repository: https://github.com/GwennanGiraud/Implications-of-synanthropic-female-macaque-sterilization.

Declarations

Consent for Publication All authors and any responsible authorities at the organization where the work was carried out have consented to manuscript submission before the work is submitted.

Inclusion and Diversity Statement The author list includes contributors from the location where they conducted the research, who helped collect and interpret the data, and manage the long-term project.

Consent to Participate Not applicable.

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Authors and Affiliations

Gwennan Giraud[1,2] · **I. Nengah Wandia**[3] · **Alain Hambuckers**[1] · **Fanny de Thier Nagelmackers**[1] · **Stefan Deleuze**[4] · **Marie-Claude Huynen**[1] · **Fany Brotcorne**[1]

✉ Gwennan Giraud
gwennangiraud@hotmail.com

[1] Research Unit SPHERES, Department of Biology, Ecology and Evolution, Faculty of Sciences, University of Liège, 4020 Liège, Belgium

[2] Technological Primates Research Group, Max Planck Institute for Evolutionary Anthropology, 04103 Leipzig, Germany

[3] Primate Division of Natural Resources and Environment Research Center, Faculty of Veterinary Medicine, Universitas Udayana, Denpasar 80361, Bali, Indonesia

[4] Research Unit FARAH, Equine and Companion Animal Reproduction Pathologies Clinic, Faculty of Veterinary Medicine, University of Liège, Sart-Tilman, 4130 Liège, Belgium