



# Direct Stacked Investment Is a Flexible Reproductive Strategy for Female *Colobus vellerosus*

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## Abstract

Most primates produce one offspring at a time but can overlap investment in consecutive offspring (stacked investment) depending on ecological and/or social conditions. “Direct stacked investment” occurs when a female conceives and gestates a new offspring while a previous infant is still suckling. We investigate direct stacked investment in *Colobus vellerosus* by determining if there is a period of overlap between nipple contact with a female’s first infant and gestation of her subsequent infant. We then investigate the effect of male group-membership and stability on stacked investment to test the hypothesis that stacking investment is a female strategy to avoid infanticide. We collected scan data to record when an infant was in nipple contact from 16 females in four groups of *C. vellerosus*, from May 2012 to May 2013 at Boabeng-Fiema Monkey Sanctuary in Ghana. We studied three group types, stable multimale, multifemale; unstable multimale, multifemale; and stable unimale, multifemale. Eight of our study females directly stacked investment. The frequency of direct stacked investment varied significantly among the group types. Stacked investment was due to earlier conception rather than delayed weaning, with females in stable multimale groups conceiving a subsequent infant earlier than those in unstable multimale groups. The timing of conception did not differ between stable unimale groups and either unstable or stable multimale groups. There was no difference in time to last nipple contact among group types. These results do not support the predictions of the infanticide avoidance hypothesis, but a larger sample size would help to test the hypothesis more comprehensively. Delayed conception by females in unstable groups may be infanticide avoidance, however, if it allows time for females to spread paternity certainty among males. Alternatively, females in unstable groups may be under stress or experience reduced feeding time due to frequent male–male agonistic interactions, both of which can suppress female ovulation. This study contributes to a growing body of research that explores flexibility in infant investment strategies, particularly in relation to external factors such as male group membership and stability.

**Keywords** *Colobus vellerosus* · Direct stacked investment · Female reproduction · Infanticide avoidance · Male group membership

## Introduction

Female mammals invest heavily in their offspring through gestation and lactation (reviewed in van Noordwijk *et al.* 2013). The most energetically costly form of female investment in mammals is lactation (Altmann and Samuels 1992; Boyce 1988; reviewed in Wade and Schneider 1992). *Female investment* in an offspring increases an infant's chances of survival, at the expense of the mother's future reproductive output (Trivers 1972) and is typically in the form of gestation and lactation. *Female care* is less energetically costly than gestation and lactation and is typically in the form of carrying, providing protection from predators and conspecifics, food-sharing, and providing learning opportunities. Female care also increases an infant's chances of survival (reviewed in van Noordwijk 2012).

Among diurnal, group-living primates the association between a mother and her offspring typically goes well beyond lactation and involves extensive periods of care (reviewed in van Noordwijk 2012). Females can optimize their reproductive success by continuing to care for their prior offspring while gestating and lactating for the next one, which van Noordwijk (2012) termed "stacking investment." Some female primates take this one step further and invest directly in two offspring at the same time, by becoming pregnant while still suckling their current infant (*Papio anubis*: Nicolson 1982; Rowell 1966; *Papio cynocephalus*: Altmann 1980; *Pan troglodytes*: Pusey 1983; *Ateles paniscus*: Symington 1987; *Trachypithecus francoisi*: Gibson and Chu 1992; *Macaca fuscata*: Tanaka 1992; *Semnopithecus* spp.: Borries *et al.* 2001; *Pongo pygmaeus*: van Noordwijk *et al.* 2013). Van Noordwijk (2012) does not include this pattern of directly overlapping investment in offspring in her definition of stacked investment.

During lactation, most mammals go through a temporary period of postnatal infertility, called lactational amenorrhea, during which ovulation is suppressed and conception is not possible (reviewed in McNeilly 2001; Recabarren *et al.* 2000; Williams 1986; Wilson 1992). Two mechanisms are at play in lactational amenorrhea: one hormonal and one energetic. Hormonal suppression of ovulation is driven by suckling stimulation that suppresses gonadotropin hormone secretion and prevents normal follicular development and ovulation (Ellison 1990, 2001; Short 1976). Energetic suppression of ovulation is driven by the high energetic requirements of lactation that signal to the body that there is not enough energy to sustain a pregnancy (Lee 1987; reviewed in von Borell *et al.* 2007). The observation that some primate females overlap the gestation of a new offspring, while suckling the previous offspring, raises questions about the assumption of a strict period of lactational amenorrhea for nonhuman primates, a concept that arose from observations based primarily on captive populations (e.g., McNeilly *et al.* 1981; Recabarren *et al.* 2000; Williams 1986; Wilson 1992). The notion of lactational amenorrhea is particularly important in explanations of male infanticide as an adaptive strategy, because infanticide is considered adaptive only if the female whose infant was killed (and hence stopped nursing) begins cycling more quickly than she would have if her infant had survived (Altmann *et al.* 1978; Hrdy 1974, 1979; reviewed in Palombit 2012, 2015).

In addition to female physiological condition, females' social environment, particularly male group membership and male–male competition, can influence the timing of reproductive events, rates of conception, and levels of investment in offspring. Male–

male competition for access to fertile females can be intense and is often expressed through events such as male immigration or fluctuations in male dominance rank. When a new male(s) immigrates into a group, females can exhibit elevated faecal glucocorticoid levels (Alberts *et al.* 1992; Carnegie *et al.* 2011; Palombit *et al.* 2000; Sapolsky 1993), indicative of physiological stress (Beehner *et al.* 2005), which can lead to abortion (Beehner *et al.* 2005; Beehner and Lu 2013; Pereira 1983) and disruption of ovulatory cycles (Beehner and Lu, 2013; Goodall 1986). High glucocorticoid levels can also have a direct effect on female rates of reproduction and levels of investment in offspring because they can cause irregularities in the ovulatory cycle and pregnancy failure in some primate species (Abbott *et al.* 1986; Adams *et al.* 1985; Cameron 1997; Harcourt 1987; Sapolsky 2002; Wasser and Starling 1988), and can affect body condition, milk production, and the timing of reproductive events (Dobson *et al.* 2012; Kalantaridou *et al.* 2004; Sapolsky 2002; reviewed in Varley and Stedman 1994 and Xiao and Ferin 1997). These effects can be the result of male aggression directed at the female or the threat of infanticide that these males pose (Beehner *et al.* 2005; Bulger and Hamilton 1987; Busse and Hamilton 1981; Collins *et al.* 1984; Palombit *et al.* 2000; Tarara 1987), and they indicate that females can respond to external events, including male behavior, by shifting the timing of reproduction and/or level of investment in offspring.

Abrupt termination of suckling in the context of male takeovers has been documented in primate species and is suggested to be a female infanticide avoidance strategy (Fairbanks and McGuire 1987; Palombit 2012; Teichroeb and Sicotte 2008; Zhao *et al.* 2011). This abrupt termination of suckling ends females' ability to directly stack investment, and therefore may explain some variation in the occurrence of direct stacked investment. The occurrence of infanticide may be lower in multimale, multifemale groups for a number of reasons: because the putative sire may be present to protect the infants; because males benefit less from killing infants when they are not able to monopolize access to females; or because females may have mated with multiple males, thus spreading paternity probability (Borries and Koenig 2000; Hausfater and Hrdy 1984; Leland *et al.* 1984; Newton 1988; Newton and Dunbar 1994; van Schaik 2000; van Schaik *et al.* 2004). This lower risk of infanticide in multimale, multifemale groups likely applies primarily to stable groups, which have more than one resident male but with a clear dominant male, where the risk of male takeover may be low and females may have the opportunity to spread paternity estimates among multiple males. Conversely, in unstable groups, which have more than one resident male and where male dominance relationships are not settled, the risk of male takeover may be high, thus increasing the risk of infanticide. If the males in these unstable groups are recent immigrants, the risk of infanticide can increase as females may not have had the opportunity to mate with and spread paternity estimates among these new males.

In this study, we build on van Noordwijk's (2012) definition of stacked investment, by adding conception and gestation of a new offspring, while still having a prior infant in nipple contact, to her original definition. We term this "direct stacked investment." We document the occurrence of direct stacked investment in *Colobus vellerosus* and investigate the timing and overlap of reproductive events (cessation of nipple contact, resumption of cycling, conception, and gestation) in relation to male group membership, the stability of male membership, and the risk of infanticide. We hypothesize that

stacked investment is an infanticide avoidance strategy and is impacted by male group membership and the stability of relationships among those males. Per the infanticide avoidance hypothesis, we predict that females in stable groups are more likely to stack investment owing to the low risk of infanticide posed by male(s) in stable groups. Because the risk of male takeover and thus infanticide is high in unstable groups, particularly if the males recently immigrated and females have not yet had an opportunity to mate with them, we predict that females in unstable groups will stack investment less than females in stable groups and will abruptly terminate suckling their offspring to reduce the risk of infanticide.

## Methods

### Study Species

*Colobus vellerosus* show no strict mating or birth seasonality (Teichroeb and Sicotte 2008). Females show considerable flexibility in the duration of nipple contact with their infants (range: 275–640 days, mean: 409 days, median: 436 days; Crotty 2016) and in the length of their interbirth intervals (range: 8–20.8 mo, mean: 17.8 mo when infants survive to nutritional independence; and range: 8–18.5 mo, mean: 11.9 mo when infants did not survive to nutritional independence; Vayro *et al.* 2016). Females in our study population live in more than one type of social context. Groups can be unimale, multifemale, or they can be multimale, multifemale (Wong and Sicotte 2006), and male incursions and takeovers are common (Sicotte *et al.* 2015). Females frequently reproduce in their natal group but sometimes disperse to other bisexual groups when their group is experiencing unstable male membership (Teichroeb *et al.* 2009) or male takeover (Sicotte *et al.* 2015). If females do not disperse, they can spend considerable time in unstable groups in which multiple males fight over dominance status or extra-group males try to enter the group and oust the resident male(s) (Sicotte *et al.* 2015). These takeovers often result in male attacks on infants and infanticide. Abrupt termination of suckling when a new male(s) enters a group has been observed and is considered a strategy to reduce the risk of infanticide (Fairbanks and McGuire 1987; Palombit 2012; Teichroeb and Sicotte 2008; Zhao *et al.* 2011).

With the help of six trained assistants, we collected data on one unimale, multifemale group and three multimale, multifemale groups of wild *Colobus vellerosus* at the Boabeng–Fiema Monkey Sanctuary (BFMS), a 192-hectare forest fragment in Central Ghana. The *C. vellerosus* at BFMS have been the subject of ongoing study since 2000, under the direction of Dr. P. Sicotte. Further detail on the site and its colobus population is described in Saj *et al.* (2005), Sicotte *et al.* (2015), Teichroeb *et al.* (2009, 2011), and Wong and Sicotte (2006).

We spent 5820 contact hours with the four groups of *Colobus vellerosus* from May 2012 to May 2013. We collected scan samples every hour, 6 days per week, from 06:00 to 14:00 h on 18 focal females in the four groups. At each scan we recorded whether an infant was in nipple contact. The number of scans varied across females, as we analyzed only those time periods in which a female was pregnant and/or had an infant in nipple contact. We were not able to determine suckling or the intensity of suckling (nutritive vs. nonnutritive suckling; Tanaka 1992), so we use “nipple contact”

as a proxy for suckling (Borries *et al.* 2014). Whether nipple contact is an appropriate measure of direct investment in an infant is unclear, because it is difficult to determine if time spent in nipple contact represents actual suckling rate, and because nipple contact does not give information about the amount of milk being transferred (reviewed in Borries *et al.* 2014). However, milk transfer may continue as long as nipple contact occurs (Reitsema 2012), and faster growth rates are associated with higher rates of suckling (Lee 1996), which suggests that nipple contact can provide an inferential measure of female investment (reviewed in Borries *et al.* 2014; *cf.* Badescu *et al.* 2016). Even when an infant is able to survive on solid food alone, milk may still be a nutritional supplement that allows the infant to allocate more energy to growth and even to social activities, such as play (Berghänel *et al.* 2015).

## Data Analysis

We report interbirth interval values from two data sets. We first report updated values for life-history variables. These values are converted from days to months using 30.4 days in a month, which is the mean month length in a regular year. For this analysis we use data collected in this study, plus Teichroeb and Sicotte (2008), and our long-term BFMS data set (2004–2011) to calculate mean interbirth interval when an infant survived and when an infant died, and age at first birth ( $N = 11$ ,  $N = 9$ ,  $N = 8$ ). These values were previously reported in Vayro *et al.* (2016) but are more precise and therefore the values presented in this article should be used for reference. We then report interbirth intervals for 16 of the 18 focal females in our study. We include only the 16 females that conceived during the study and use this second data set for all remaining results. We determined pregnancy as outlined in Vayro *et al.* (2016), using both hormonal and observational data. For 14 females we calculated day of conception by subtracting the mean gestation length for *Colobus vellerosus* (168.5 days; see Results) from the day of parturition. For the other two females we used the rise in fecal estradiol and fecal progesterone to determine ovulation and the day of conception, and the sharp decrease in fecal estradiol and fecal progesterone to determine the day of parturition (Vayro *et al.* 2016). We categorized a female as having “direct stacked investment” if she had an infant in nipple contact during the conceptive cycle and gestation of her subsequent infant.

We used birthdates to calculate infant age at the time of the first infant’s last nipple contact. Trained local assistants and researchers recorded all infant births within 1–2 days throughout the study when possible. When an observer was not present immediately following a birth, trained researchers assigned approximate ages for all individuals (within 1–3 mo) based on body size. Our sample consists of nine infants with approximate ages and seven with exact ages.

All of our groups were multifemale, with variable male group membership. Our categorical naming system focuses on the males in each group, because all groups were multifemale and it is the male group membership that distinguishes the groups from one another. We classified groups as stable unimale, multifemale; stable multimale, multifemale; and unstable multimale, multifemale. We define a stable unimale group as having one resident male and not experiencing male incursions or (attempted) takeovers for the length of the study. We define a stable multimale group as having more than one resident male, but with a clear dominant

male, and the group did not experience male incursions, (attempted) takeovers, or internal dominance struggles for the length of the study. The stable multimale group in this study included five males, one dominant and four nondominant males. We define an unstable multimale group as having more than one resident male, but male dominance relationships were not settled, as indicated by regular bidirectional agonistic interactions between the resident males and/or incoming males. The unstable multimale group in this study included between five and eight males. At the start of the study this group was unimale, multifemale, but an all-male band immigrated into the group early in the study period, making it an unstable multimale group. The variation in number of males was due to male deaths throughout our study. We had no unstable unimale, multifemale groups in our sample, which we defined as a group that experienced male incursions or (attempted) takeovers, with the incurring male(s) staying < 1 mo.

We used a two tailed Fisher's exact test ("fisher.test" in R base code, R version 4.0.0) to determine whether female stacked investment differed among group types. We excluded the four cases in which infants died before the female conceived her next infant from this analysis. We also conducted a survival analysis to determine whether the differences in stacked investment between group types could be attributed to females ending nipple contact with their first infant later or conceiving their second infant earlier, or both. Using a survival analysis allowed us to include infants that died before weaning in the model as censored data points. First, we graphed Kaplan Meier curves for each variable using the `cox.zph` function (R package "survival"; Therneau 2015; Therneau and Grambsch 2000) to assess the proportional hazards assumption. For time to next conception we then used a Cox proportional hazards regression to determine if there were differences between groups. We used the `coxph` function (R package "survival"; Therneau 2015; Therneau and Grambsch 2000) and tested for significance using the log rank test. For both models, survival intervals begin at the first infant's birth. We computed statistical analyses in R version 3.6.1.

## Ethical Note

Our data collection methods complied with the rules of the University of Calgary's Animal Care Committee and with the laws of Ghana. The authors declare that they have no conflict of interest.

**Data Availability** The data sets generated and analyzed during the study are available in this publication, and further details are available on reasonable request from the corresponding author.

## Results

### Life-History Variables

Gestation length was 159 days (5.2 mo  $\pm$  0 days) and 178 days (5.9 mo  $\pm$  3 days) for the two females from which we had hormonal measures of pregnancy, giving a mean

gestation length of 168.5 days (5.5 mo). For females whose infants survived to nutritional independence, the mean interbirth interval was 16.5 mo (range = 8.3–24.0 mo,  $N = 11$ ). For females whose infants did not survive to nutritional independence, the mean interbirth interval was 11.4 mo (range = 8.0–17.1 mo,  $N = 9$ ). The mean age at first birth was 5.9 yr (range = 4.7–6.7 yr,  $N = 8$ ).

### Patterns of Direct Stacked Investment

Out of 16 females that conceived during the study period, 8 had an infant in nipple contact when they conceived and gestated the subsequent offspring, i.e., directly stacked investment. Four females ceased nipple contact before their next conception. Of these four females, one was observed with an infant in nipple contact on the estimated day of conception but not after the day of conception (Table I), which we did not consider stacked investment. Four females' infants disappeared/died before termination of suckling and conception of their next infant. The mean age at which suckling was terminated was 15.4 mo (range = 10.5–23.2 mo,  $N = 8$ ) for infants whose mother stacked investment and 15.6 mo (range = 11.4–19 mo,  $N = 4$ ) for infants whose mother did not stack investment. Three females, all in stable unimale groups, were primiparous at the start of the study. One primiparous female's infant died before last nipple contact, one female stacked investment, and the third female did not stack investment (lactation length: 23.2 mo and 11.4 mo, respectively).

### Effect of male group membership and group stability on stacked investment

All females in stable multimale groups stacked investment ( $N = 5$ ). We did not observe any cases of direct stacked investment in unstable multimale groups: two females did not stack investment, two females' infants died before last nipple contact, and one female ceased nipple contact on the day of conception ( $N = 5$ ). In the stable unimale groups, three females stacked investment, one female did not stack investment, and two females' infants died before last nipple contact ( $N = 6$ ). The frequency of direct stacked investment varied significantly among the group types (Fisher's Exact Test,  $P = 0.01$ ,  $N = 12$ ) (Table II). The mean infant age at which suckling was terminated was 14.7 mo in stable multimale groups (range = 10.5–17.1,  $N = 5$ ), 17.8 mo in unstable multi-male groups (range = 15.6–19,  $N = 3$ ), and 15.3 mo in stable unimale groups (range = 11.4–23.2,  $N = 4$ ).

Visual assessment of the Kaplan–Meier curves indicate that the proportional hazards assumption was not met for days to last nipple contact analysis; therefore male group composition and stability do not strongly influence the timing of last nipple contact (Fig. 1). A chi-square test comparing the Kaplan–Meier curves for timing of last nipple contact was not significant ( $\chi^2 = 1.4$ ,  $P = 0.5$ ). The proportional hazards assumption was met for the days to next conception analysis and the Cox proportional hazards model indicated that the number of days to next conception varied significantly between group types (log rank test = 7.79,  $P = 0.02$ , Fig. 2). Females conceived their second infant earlier in stable multimale groups compared to unstable multimale, where being in an unstable multimale group was associated with a 72% reduction of the conception hazard ( $P = 0.02$ , Fig. 2). The timing of conception did not differ between stable unimale groups and either stable multimale or unstable multimale groups (Fig. 2).

**Table 1** Summary of reproduction in female *Colobus vellerosus* at Boabeng–Fiema Monkey Sanctuary from May 2012 to May 2013

Female	Group	Group type at time of second conception	Months between conception and last nipple contact	First infant age in months at last nipple contact	Female parity at time of first infant	Number of scans per female
BE	RT	Stable multimale, multifemale	5.2	<b>10.5</b>	Multiparous	526
BL	RT	Stable multimale, multifemale	4.4	13.7	Multiparous	510
FV	RT	Stable multimale, multifemale	2.8	17.1	Multiparous	426
SU	RT	Stable multimale, multifemale	3.2	16.8	Multiparous	548
TR	RT	Stable multimale, multifemale	4.4	15.2	Multiparous	474
CT	SP	Unstable multimale, multifemale	0.0	15.6	Multiparous	647
SA <sup>a</sup>	SP	Unstable multimale, multifemale	-6.7	<b>2.8</b>	Multiparous	573
SE	SP	Unstable multimale, multifemale	-0.6	18.9	Multiparous	590
VE <sup>a</sup>	SP	Unstable multimale, multifemale	-2.3	<b>2.2</b>	Multiparous	543
XE	SP	Unstable multimale, multifemale	-0.5	19.0	Multiparous	638
IS <sup>a</sup>	WT	Stable unimale, multifemale	-1.8	<b>9.8</b>	Primiparous	594
VM	WT	Stable unimale, multifemale	4.9	<b>23.2</b>	Primiparous	574
XY	WT	Stable unimale, multifemale	-7.2	<b>11.4</b>	Primiparous	559
CR	WW	Stable unimale, multifemale	4.2	<b>12.8</b>	Multiparous	391
IT	WW	Stable unimale, multifemale	4.4	<b>13.7</b>	Multiparous	343
JN <sup>a</sup>	WW	Stable unimale, multifemale	-0.9	4.3	Multiparous	385

A negative number in the “Months between conception and last nipple contact” column indicates that last nipple contact occurred before the day of next conception and the female did not stack investment. A positive number indicates that last nipple contact occurred after the day of next conception and the female did stack investment. Infant ages in bold are exact age; all other infant ages are approximate.

<sup>a</sup> Indicates that the female’s infant died/disappeared before termination of suckling.

## Discussion

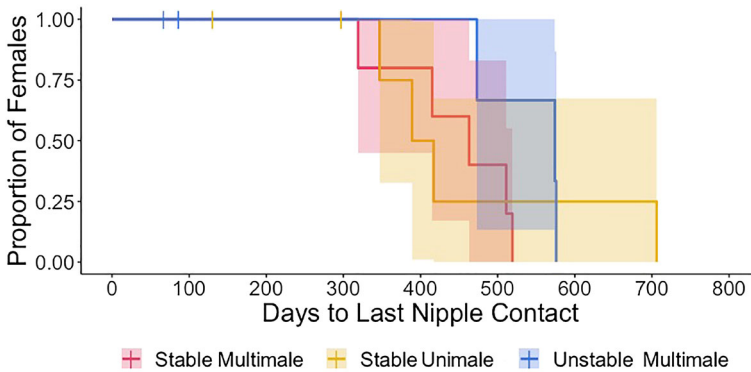
Eight out of the 12 study females whose infant survived to last nipple contact directly stacked investment for a period ranging from 2.8 mo to 5.2 mo. All females that stacked



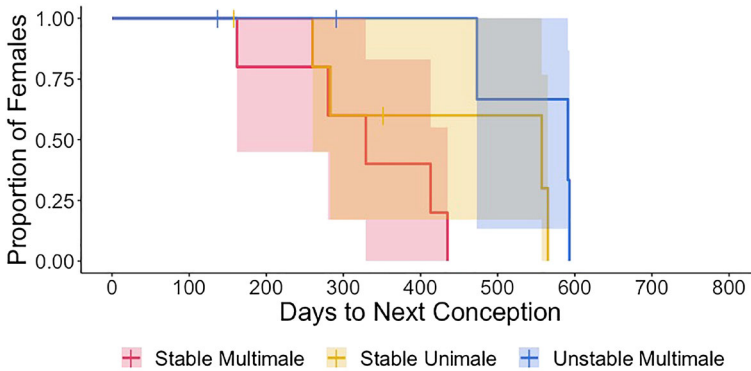
**Table II** Frequency of stacked investment in female *Colobus vellerosus* living in different group types at Boabeng-Fiema Monkey Sanctuary from May 2012 to May 2013

Stacked investment	Stable unimale, multifemale	Stable multimale, multifemale	Unstable multimale, multifemale
Yes	3 females	5 females	0 female
No	1 female	0 females	3 females

The frequency of direct stacked investment varied significantly among the group types (Fisher’s Exact Test,  $P = 0.01$ ,  $N = 12$ ).



**Fig. 1** Days to last nipple contact in female *Colobus vellerosus* at Boabeng–Fiema Monkey Sanctuary from May 2012 to May 2013. Kaplan–Meier curves and 95% confidence intervals showing the proportion of females with an infant in nipple contact (y-axis) after a given number of days since the infant’s birth (x-axis).



**Fig. 2** Days to next conception in female *Colobus vellerosus* at Boabeng–Fiema Monkey Sanctuary from May 2012 to May 2013. Kaplan–Meier curves and 95% confidence intervals showing the proportion of females who had not yet conceived the second infant (y-axis) after a given number of days since the first infant’s birth (x-axis).

investment conceived their subsequent infant after the first 5 mo of nipple contact with their first infant. This suggests that there may be a limit on females' ability to conceive and thus stack investment in the first 5 mo after an infant is born. However, the length of nipple contact in *Colobus vellerosus* ranges from 9.0 mo to 21.1 mo (mean = 13.5 mo) (Crotty 2016). This leaves between 4 and 16 mo in which females with an infant in nipple contact could reconceive. Therefore, after the first 5 mo with an infant in nipple contact, the effects of suckling stimulus on the resumption of cycling in our study population may be small. We observed a high occurrence of direct stacked investment in stable multimale groups and females in these groups conceived earlier than those in unstable multimale groups. Group type was not a good predictor of time to last nipple contact and there was no difference in time to last nipple contact between females in any group type. The timing of conception did not differ between stable unimale groups and either unstable multimale or stable multimale groups. Of the four females that did not stack investment, three (CT, SP, and XE) had their next conception within 1 mo of last nipple contact. This timing is within the range of error for our conception date calculations, [gestation length: 159 days (5.2 mo  $\pm$  0 days) and 178 days (5.9 mo  $\pm$  3 days)] (Vayro *et al.* 2016) and it is possible that these three females conceived a subsequent infant while their previous infant was still in nipple contact. However, we chose to err on the side of caution with these three females and therefore considered them as having not stacked investment. Further research, with more hormonal data on the exact timing of pregnancy, could help to clarify these results.

Abrupt cessation of suckling does not appear to be a female strategy to reduce the risk of infanticide based on our results, as the timing to last nipple contact did not differ between females in different group types. Instead, females in stable multimale groups conceived earlier than did those in unstable multimale groups. These findings suggest that variation in the occurrence of direct stacked investment in this population is not due to infanticide risk in the way we originally predicted. However, our result that females in unstable multimale groups conceived later than those in stable multimale groups suggests that female's may reduce the risk infanticide by delaying conception rather than weaning abruptly. Therefore, this delayed conception could lower the risk of infanticide for females in unstable groups if it allows them to mate with all the males their group. Females in unstable multimale groups may spread paternity probability among many males to maximize protection possibilities from potential and actual fathers (Clarke *et al.* 2009; van Schaik 2000). Preliminary data from *Colobus vellerosus* (Vayro *et al.* 2017) suggest that females in unstable multimale groups solicit copulations from all males more than those in stable multimale groups, further supporting this idea. Additional investigation of these concepts, using a larger sample size, is needed.

Instability in male group membership can affect female reproduction in ways beyond female investment decisions. Females in unstable groups may be under stress and may experience an increase in the hormones associated with stress due to frequent male–male agonistic interactions. These stress hormones can suppress ovulation (Beehner *et al.* 2005; Beehner and Lu 2013; Goodall 1986). Females may also experience reduced feeding time in unstable groups because they are being vigilant or are displaced by competing males, which can make it difficult for them to meet their daily nutritional requirement (Emery Thompson *et al.* 2014). These types of stressors can lead to overall poor body condition and a subsequent reduction in reproductive capabilities. Females in unstable groups may have longer time to postpartum recuperation (Mas-Rivera and Bercovitch 2008) and this may prevent them from investing in two offspring simultaneously. Alternatively, females in stable groups may experience lower stress levels and comparatively uninterrupted feeding

time, which could translate into better maternal condition, freeing energy that can be invested in future offspring.

If male group membership and stability alone predicted female stacked investment, we would have expected females in stable unimale groups to stack investment more. We found a wide range in months between last nipple contact and conception in stable unimale groups (−7.2 to +4.9 mo). This large range could help explain females' preference for living in stable unimale groups, with a prime male (Teichroeb *et al.* 2012), because they may have more opportunities to be flexible in their investment and care of offspring. Had we examined only multimale groups it may have appeared that male behavior is the primary driver of female interbirth intervals.

Lactation lengths of the primiparous females with surviving infants were 23.2 mo and 11.4 mo. The 23.2-mo lactation length is the longest of all study females that stacked investment, while the 11.4-mo lactation length is the shortest for all study females that did not stack investment. These primiparous females show great variation in their lactation length, which is not unlike that of the multiparous females in our study and may further support the idea that female *Colobus vellerosus* have considerable flexibility in their levels of offspring investment.

The results of this study are limited owing to our small sample size but show a need for further work on the predictors of direct stacked investment. In particular, factors like food availability, female condition, female age, or female rank may be affecting females' opportunity or ability to stack investment. Further studies with a larger data set to explore the effect of male group membership and group stability, while considering other factors such as female rank, infant handling, or food availability, could help clarify our results.

In this study, we define “direct stacked investment” and explore the social conditions that may be influencing females' ability to invest directly in more than one offspring at the same time. Through defining and exploring the social context of female direct stacked investment, we contribute to a growing body of research that explores females as flexible and opportunistic actors (Hrdy 2000) in their infant investment strategies, particularly in relation to external factors such as male group membership and interactions between males.

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**Author contributions** JV conceived and designed the study, conducted fieldwork, analyzed the data, and wrote the manuscript. TZ contributed to the hormonal analysis and provided editorial advice. LF contributed to the study design and provided editorial advice. AC conducted fieldwork and contributed to the data set. SF conducted fieldwork, contributed to the data set, and provided editorial advice. PS conceived and designed the study and provided editorial advice.

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