I- Introduction

Reproductive synchrony is the tendency of individuals to achieve particular phases of the reproductive cycle, such as birth, at the same time as other members of their population. It is a very common phenomenon that has been documented for a wide variety of living organisms, from plants to animals, including birds, mammals and even humans (Ims 1990a). Synchronizing reproduction could have a variety of benefits. Two of the most common explanations relate to reducing predation risk and increasing food availability. In the first case, it has long been documented that reproductive synchrony might reduce predation (Darling 1938), (Ims 1990b). This might occur through two mechanisms. First, if many adults breed at the same time, it increases the protection of the offspring by increasing the number of adults involved in collective defence (Reference...). Second, by increasing the number of offspring at the same time in a population, the probability for each infant to be killed by predation is reduced, leading to the 'dilution effect' (Reference...). In the second case, seasonal variation in food availability can lead to annual patterns of reproductive synchrony (Reference...). For example, seasonal breeding can help to minimize the energetic cost of reproduction by synchronizing birth with the period when food is most abundant (Brockman & van Schaik 2005a).

Patterns of reproductive synchrony are usually assumed to be uniform across populations. However, in socially-structured species with spatially- and socially-differentiated groups, reproductive synchrony may be more complex. Here, patterns of synchrony may be driven primarily at the group level. Such group-level synchrony might emerge in heterogeneous environments where groups are exposed to different levels of predation risk and/or have variable access to key seasonally-available food resources. Moreover, studies of other biological phenomenan at multiple population scales, such as small population networks and metapopulations (Sutherland 1996, Persson & de Roos 2003, Ranta et al. 2008), indicate that patterns of reproductive synchrony at the group level may lead to complex emergent patterns at the population level.

One of the strongest candidates for driving reproductive synchrony in groups in structured populations may be infanticide. Infanticide is a reproductive strategy, most commonly seen in polygynous mammals, in which males kill the lactating offspring of other males to bring the females back into oestrus (Hausfater & Hrdy 1984, van Schaik & Janson 2000). In socially-structured populations, this usually occurs when a male who has recently immigrated into a social group seizes the alpha-male position and kills the infants of the former male. This pattern of behaviour clearly has the potential to synchronise female reproduction in the troop (Janson & Verdolin 2005), and may also influence reproduction in other troops through subsequent patterns of male migration.

This study aims to explore the role of infanticide in reproductive synchrony at both the group and population level. To do so, it adopts a theoretical approach using an individual-based model. With increasing computational power, individual-based models have become more and more widely used in ecology (Judson 1994, Grimm 1999). It is an ideal approach for a study of this nature, since it allows us to characterize precisely the role of each individual represented in the model, and to observe the emerging results at all the different levels, from the individual to the group to the population (Sumpter & Broomhead 2001, Ovaskainen & Hanski 2004). Ours is a general model of infanticide in a socially-structured population. Nevertheless, for the purposes of this study, it is parameterised for primates, specifically baboons (*Papio* spp). Baboons live in socially-structured populations and the ecology, behaviour and life history of this taxon – including infanticidal behaviour – has been well-studied, providing the necessary data for accurate model parameterisation (Collins et al. 1984, Palombit et al. 2000, Henzi & Barrett 2003). Our main objective is to verify if infanticide can lead to synchrony in births and other related processes, such as the migration of males. We then explore these patterns in both non-seasonal and seasonal environments. Finally, we assess whether the effects of infanticide and seasonality within groups can lead to the emergence of complex patterns of synchrony at the population level.

II- Model implementation and methods

II.1- Model design

We built a discrete-time model where each individual is explicitly represented. This individual-based modelling approach simulates a population of baboons to investigate the effect of infanticide on synchrony in reproduction and other related processes. A baboon population is composed of several independent social groups or ‘troops’, four in the model, connected by the migration of males between the troops. A troop is composed of three different classes of individuals: resident adult females, immatures (of both sexes), and adult males who come and go through migration. In the model, individuals in each class are represented according to their age and a state. The different possible states depend on the class of individual.

An adult female can be in four different states, describing a simplified reproductive cycle:

- Cycling: with a duration of 35 days, this state corresponds to the oestrous cycle of a baboon.
- Mating: during the oestrous cycle, at ovulation, the female will copulate if a male is present in the group. This event is considered to be instantaneous, but its outcome determines the rest of the cycle. If the female does not conceive, she finishes her oestrous cycle normally. On the other hand, if she conceives, the oestrous cycle is interrupted and the female

becomes pregnant.

- Pregnant: this state lasts six months. At the end of the pregnancy period, the female gives birth to one infant and enters the lactating state.
- Lactating: this state lasts 18 months. At the end of the lactation, the infant is weaned, and the female resumes cycling within a variable period of time, 70 to 140 days (2 to 4 oestrous cycles) drawn at random from a uniform distribution .

An immature of either sex can be in two different states:

- Infant: an infant is an immature before weaning. This state corresponds to the lactating state of the mother and lasts 18 months.
- Juvenile: after weaning, an immature is called juvenile until it reaches maturity.

Patterns of growth and mortality for juveniles and adults in the model follow those described in the literature (following Altmann & Alberts 2003). Thus, the time needed to reach maturity depends on the sex of the juvenile and the size of the group. Group size is important because density-dependent processes promote early maturity in a small (low density) troop. Infants have a higher probability of death at each step than juveniles. The mortality rate of juveniles is dependent on the density as well, increasing with the size of the group. The mortality rate of females is considered do be constant over time and across the different states. When an immature animal reaches maturity, its pattern of recruitment depends on the sex. Females are directly recruited to the natal group, whereas males always leave the group and are recruited to an external pool of males from where they will immigrate into another troop (see below).

A male can be in three different states, and the states of males in a group determine the social structure of the group:

- Outside a group: the male is considered a solitary male that can immigrate into a group. In the model, all solitary males are modelled in the same external pool of males but are all behaving independently.
- Subordinate in a group. In this state, the male has the possibility to leave the troop, or to try to take over the dominant (alpha-male) position.
- Dominant in a group. At any time in a troop, only one male can take the alpha-male position. This position is always occupied. On very rare occasions, it is possible that only a single male is present in the troop, but should that male die his position is quickly re-occupied by an immigrating male.

Migration is a fundamental process in the model since it plays an important role in infanticide. As all males are recruited to the outside pool of males, a male can only enter a group through migration, and always avoids the natal troop. At each time step, the probability of male immigration into a troop or emigration from the troop depends on the attractiveness of the troop. This in turn depends on the operational sex ratio, i.e. the number of cycling female per male present (following Alberts & Altmann 1995). That is to say, the more cycling females and the fewer males, the more attractive the group. If a group is attractive, males from the outside are more likely to enter it and males in the troop are less likely to leave it. When a male leaves a troop, he joins the external pool before going elsewhere (there is no direct migration from one troop to another). When a male enters a troop, he enters as a subordinate. He then either stays subordinate or challenges the alpha-male to take-over the dominant position.

The challenger can be either a resident subordinate male or one that has just arrived through immigration. The probability of challenge is directly dependent on both the respective ages of the alpha-male and the challenger (age determines the strength of the individual, see Annex 1, following Alberts et al. 2003), and the origin of the challenger (a new immigrant is more likely to challenge the alpha-male compared to a resident of the same strength, following Alberts & Altmann 1995). A subordinate will only challenge the alpha-male if he is strong enough compared to the dominant. The outcome of the challenge depends on the strength of the contestants, modulated with stochastic processes to allow weaker males a small probability of victory by chance. The loser has the possibility to stay in the troop as a subordinate. If a challenger takes over the dominant position, he then has a probability to commit infanticide.

An infanticide event occurs when the new alpha-male tries to kill all the infants. However, the ex-dominant can stay in the troop and try to protect the infants (following Palombit 2003). If an infant is killed, the mother resumes cycling in a shorter period of time than at the usual end of the lactation period, only 0 to 2 oestrus cycles (following Altmann & Alberts 2003). If several infants are killed during the same event of infanticide, the same number of females resume cycling at the same time, which synchronizes them.

Finally, baboons live in a variety of environments which can lead to weak patterns of seasonality in birth (e.g. Amboseli, Kenya: Alberts et al. 2005) to strong patterns of seasonality in birth (e.g. Okavango, Botswana: Cheney et al. 2004). To explore the respective effects of infanticide and seasonality on reproductive synchrony, we allowed the monthly probability of female conception to stay uniform (non-seasonal) or to vary (seasonal). To simulate this range of variation, seasonal forcing was incorporated as a simple cosine function with a period of one year and a variable amplitude. This permitted the probability of female conception to vary from a fixed value throughout the year to a function ranging from 0 to 1 depending on the time in the year.

The different parameters of the model, such as durations of periods, rates and probabilities, are set to fit as well as possible the values reported for baboons in the literature (Table 1). The population is composed of four troops. The initial composition of each troop is 20 females with a random state and age, as many infants as lactating females, no juveniles, and one dominant and one subordinate male with a random age. The random ages and states are drawn from a uniform distribution. The time step is set at five days, and one simulation covers a period of 20000 time steps (274 years).

Using these parameters, the model is validated by comparing key model outputs against observed empirical patterns in wild baboon populations. Following validation, three different situations are modelled in this study. First, control simulations with no infanticide (i.e. males do not kill infants when they become alpha-male) or seasonality (i.e. the probability of female conception remains constant in each month). Second, simulations where infanticide occurs but breeding is aseasonal. Third, infanticide occurs along with seasonality.

II.2- Methods for analysing the results

During each simulation, three different output variables were recorded at each time step: the number of births, infants killed, and immigrating males. Each output variable produced a time series that was subsequently analysed for patterns of synchrony in reproduction, infanticide and immigration, respectively. An example of time series for births is given in Figure 1-A.

Different methods are used to analyse these time series to detect the presence of synchrony. To obtain the spectrum of a time series, which gives information on the presence of one or several dominant frequencies (Figure 1-B), a Fourier analysis can be used (Zurbenko 1988). The Fourier analysis is a very powerful way of determining precisely the main frequencies (peaks) present in a signal. However, the statistical significance of these frequencies is given by the area under the peaks which is not easy to measure on a spectrum. Consequently, to determine the importance of a frequency in a time series, we have used the autocorrelation function (Figure 1-C).

Unlike the Fourier analysis which measures frequency, the autocorrelation measures the correlation between two points separated by a given lag in the time series. The autocorrelation function is the measure of autocorrelation for all the possible lags: when a peak in autocorrelation occurs for a certain lag, this lag corresponds to a noteworthy period in the time series (Brockwell et al. 1991). The autocorrelation function is less precise in determining the main frequencies, particularly when several frequencies interfere together, but it facilitates the easy measurement of the significance of a period when it is the only one present in the signal.

The approach adopted here can therefore be summarised as follows. To determine the presence of synchrony in a time series, we used the Fourier analyses. When only one frequency was present on the spectrum, we then used the autocorrelation function to measure the statistical significance of the frequency in that time series. A peak in autocorrelation is significant when it is above the 95% confidence interval for the time series as a whole (Brockwell et al. 1991). Because of the stochasticity introduced in the model, and to have some statistical robustness in our results, one simulation consists of 50 replicates with the same parameters. To compare the strength of synchrony between simulations, the maximum value of autocorrelation (ac_{max}) at the frequency detected in each time series was measured (Figure 1-C) and subsequently compared between simulations using a t-test without assumption of equal variances. Prior to this test, the ac_{max} distributions were verified for normality using a Shapiro-Wilks test. Because the result of a t-test is sensitive to sample size (even very small differences can be strongly significant with a large sample), all tests with 50 replicates per simulation were repeated with a smaller sample size of 15 replicates selected at random from the full sample.

Parameters	Value	References
	Duration of the different periods	
Cycle of a female	7Δt = 35 d	[Bentley-Condit1997]
Pregnancy period	36Δt = 6 m	[Bentley-Condit1997]
Lactation period	108Δt = 18 m	[Altmann2003]
Interbirth interval	164 ± 3Δt = 2.24 yr ± 15 d (rp)	[Altmann2003]
Age of maturity for females	365Δt = 5 yr ± dd	[Cheney 2004]
Age of maturity for males	584Δt ± dd = 8 yr ± dd	[Cheney 2004]
	Death Rates (/yr)	
Females	0,1	[Cheney 2004]
Males in a troop	0,07	[Alberts1995]
Males outside	0,11	[Alberts1995]
Juveniles	0,13 (dd)	[Cheney 2004]
Infants	0,17	[Cheney 2004]
	Other parameters	
Probability for the loser of a challenge to stay	0,75	Cowlishaw pers comm
Probability of infanticide		
male from the inside	0,05	Cowlishaw pers comm
immigrating male	0,8	Cowlishaw pers comm
Probability of protection by the ex-dominant		
against male from the inside	0,75	Cowlishaw pers comm
against immigrating male	0,8	Cowlishaw pers comm
Percentage of infant protected	0,5	Cowlishaw pers comm
Probability of conception	fix: 0.5, seasonal: 0.5 - [0:1]	Cowlishaw pers comm
Probability of immigration	$p \propto (1+f_{cycling})/(1+m_{inside}+f_{cycling})$	[Alberts1995]
Probability of emigartion	$p \propto (1+m_{inside})/(1+m_{inside}+f_{cycling})$	[Alberts1995]

Table 1: Parameters used in the model. Δt is the time step of the model (5 days). rp stand for random processes, they are used to add stochasticity in the model. dd stand for density dependence. $f_{cycling}$ *Is the number of cycling female in the troop.* m_{inside} *Is the number of males present in the troop.*

With the addition of seasonality, the signal became more complex, with several significant frequencies and possible interference between them. The autocorrelogram is thus too complex to be used to measure the significance of each frequency. We then measured the area beneath each peak in the spectrum given by the Fourier analysis to compare the influence of the different frequencies in the signal.

To study patterns of synchrony between troops, we compared the time series using the cross-correlation function (Brockwell et al. 1991). This function gives the correlation between two time series for different lags between them. The maximum of this function gives the phase difference between the time series.

Finally, to study patterns at the population level, the time series of each troop were summed to get the aggregate, population-level, time series for reproduction, infanticide and migration. Synchrony in these three aggregate time series was then assessed in the same way as for the group-level time series, as described above.

III- Results

III.1- Model validation

In order to validate the model, we assessed two different types of output from the model simulations: (1) the number of individuals per class in each troop throughout the simulation period (to obtain information on the dynamics of the troops), and (2) statistics on the general behaviour of the model, such as the immigration rates, alpha-male tenure lengths, number of challenges/take-overs, number of births, and infanticide rates. These outputs were then compared to patterns observed in wild baboons. The validation was carried out on those simulations that include infanticide and both seasonal and aseasonal breeding.

In the case of troop size and composition, the model rapidly produces a stable troop structure which at its steady state comprises 17 to 22 females, 3 to 8 males and around 30 to 35 immatures. This troop size and composition is typical of wild baboon populations (Cheney et al. 2004). In the second case, the model outputs on male immigration rate (number of males immigrating per year), alpha-male tenure length (months), and infanticide rates (% of infants killed per year) were found to compare well to the range of values in the literature (Table 2). Infanticide rate in the model is at the higher end of the observed range, but this was considered acceptable given that our primary interest in this study was to investigate how infanticide might cause synchrony, and that these patterns would likely be clearest when infanticide is relatively high. The model outputs given on Table 2 are drawn from the simulations without seasonality, but the inclusion of seasonality does not affect these values in any substantial way.

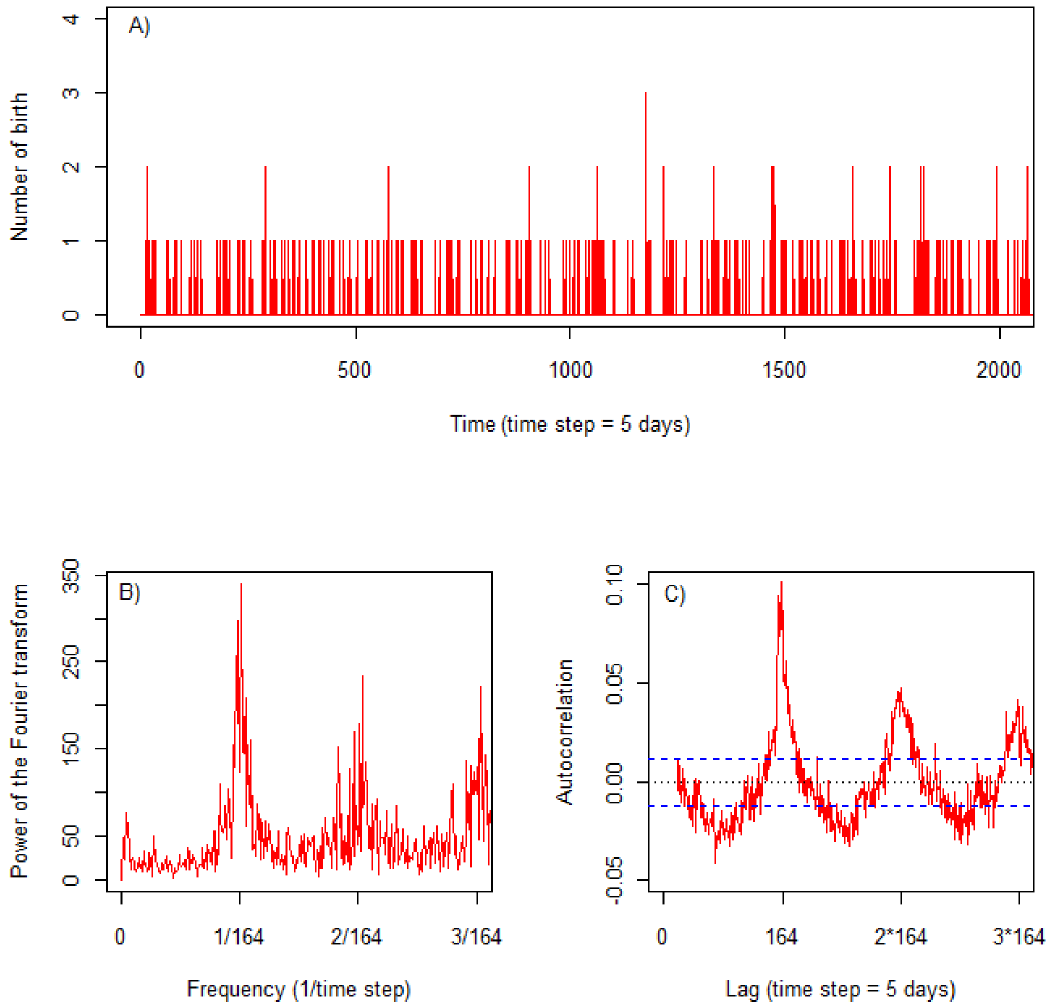

Figure 1: A) Extract of a time series for births, 2000 time steps corresponds to 27 years. Each peak represent an event of one or several births at the same time. B) Spectrum of the time series. Higher frequencies are not shown because only the noise is present. The first interesting peak, at 1/164, corresponding to the interbirth interval, shows the presence of reproductive synchrony with a period of 164 time steps. The other peaks at 2/164 and 3/164 are the harmonics of the first one, present because the time series is a complex non linear signal. C) Autocorrelogram of the time series with 95% confidence interval. The first peak with a lag of 164 time steps shows the synchrony as well. The maximum value of autocorrelation, here about 0.1, informs on the level of synchrony. The following peaks at 2 times and 3 times the interbirth interval confirm the importance of the first peak.

III.2- Control simulations

Following model validation, a control simulation was carried out to assess synchrony in reproduction and male immigration in the absence of infanticide and seasonality.

Surprisingly, even without the influence of these processes, a low level of synchrony in female reproduction occurred. This reflects the fact that with around 20 females in a troop, cycling stochastically, some females will cycle in phase simply by chance. The strength of synchrony in the simulation, given by the ac_{max} value in each of 50 replicates, has a mean of 0.064 (sd=0.006, above the 95% confidence interval). The synchrony in reproduction occurs with a period of 164 time steps (around 2.2 years), which corresponds to the interbirth interval, i.e. the average time separating two consecutive births (see Table 1). Under these simulation conditions, the autocorrelograms of the migration time series indicate that a very low level of synchrony is also present in male immigration in the same time period, i.e. the interbirth interval. In this case, mean ac_{max}=0.038 (sd=0.006, above the 95% confidence interval).

	Model Output	Previous studies [Reference]		
Immigration rate (Ind/yr)	m = 2.6, sd = 0.17	0.2 [Henzi2003]	2.4 [Weingrill2000]	6.0 [Clarke2008]
Tenure length (months)	m = 29.4, sd = 2.3	11.0 [Clarke2008]	>30.0 [Henzi2003]	44 [Collins1984]
Infanticide rate	m = 15.5, sd =1.5	0.3 [Henzi2003]	7 [Janson2000]	15 [Henzi2003]

Table 2: Statistics for the validation of the model. m is the mean value over 50 replicates, sd is the standard deviation.

Finally, no synchrony at all is present in infanticide, and no particular pattern of synchrony exists between troops. All the troops are behaving independently. Nevertheless, a low level of reproductive synchrony is still detectable at the population level, albeit weaker than that seen but lower than the one for each group separately. The mean ac_{max} = 0.057, sd=0.004, exceeds the 95% confidence interval and is normally distributed (Shapiro-Wilk test: W=0.97, n=50, p=0.22). No synchrony is present in male immigration at the population level.

III.3- The effect of infanticide at the group level

With the addition of infanticide to the model, we observed several changes at the group level compared to the control simulation.

First of all, with infanticide, we observed the presence of a significant frequency in the time series of births corresponding to the interbirth interval, as in the control (Figure 2). Importantly, the strength of synchrony was significantly stronger with infanticide than without it (Figure 3-A) (t-tests on ac_{max} values: 50 replicates, t=15.5, df=96.3, $p=10^{-16}$; 15 replicates: t=9.4, df=27.5,$p=10^{-10}$). Infanticide therefore causes a significant increase in the reproductive synchrony of baboons.

With the synchronization of female reproduction, we also observed some synchronization of male immigration in the different troops, once again at the interbirth interval (Figure 2 and 3-B). As with the sychrony in births, the sychrony in immigration was stronger in the presence of infanticide (50 replicates: t=12.6, df=97.8, $p=10^{-16}$; 15 replicates: t=6.3, df=26.8, $p=10^{-6}$). Infanticide therefore seems to increase synchrony in migration as well as reproduction.

Concerning infanticide itself, it never becomes synchronous. No particular frequency emerges in the spectrum and no lag is particularly significant in the autocorrelation function. Nevertheless, infanticide and birth events remain strongly correlated. The cross correlation between the two time series of infanticides and births shows that an event of infanticide is followed by an event of birth about 43 time steps (215 days) later, which corresponds to 35 days (one oestrous cycle) plus 180 days (6 months, the pregnancy period) (see Annex 1-A). In the same way, most infanticide events are preceded by an immigration of a male into the troop the time step before (Annex 1-B).

Since we found that infanticide increases reproductive synchrony, we investigated in more detail the effect of the infanticide rate on the level of synchrony. We explored a large range of infanticide rates, from 0% (control situation) to nearly 17%, with all other parameters remaining unchanged (the only parameter modified to simulate this range of infanticide rates was the probability of a new alpha-male making infanticidal attacks). As we might expect, the rate of infanticide had a direct effect on the level of synchrony (Figure 4).

When seasonality is added to the model, some of the patterns of synchrony change. First, with increasing seasonal forcing, reproductive synchrony tends to become more complex than before. The spectra show clearly that a new frequency appears in the signal, corresponding to a period of one year (73 time steps), due to the seasonality. However, the period of the interbirth interval also remains present across the full range of seasonality tested (Figures 5-A to C), and a qualitative comparison of the area under the peaks suggests that the interbirth interval remains the most significant period.

Further scrutiny suggests that there may also be interference between these two dominant frequencies when seasonality is strong. Evidence for this comes from the appearance of other small peaks on the spectrum (Annex 2-A). The complexity of the corresponding autocorrelogram (Annex 2-B) tends to confirm this hypothesis. Although further investigation of these interference patterns lies beyond the scope of this study, it remains clear that with seasonality in the model we have the coexistence of two periods of synchronization in reproduction, the interbirth interval and the year, giving a more complex time series than before.

Second, unexpectedly, immigration does not follow the same rhythm as reproduction. Although migration is directly related to the female cycle through the attractiveness of the troop, the seasonal forcing has absolutely no effect on immigration rates. For the whole range of seasonality tested, immigration only synchronizes at the interbirth interval (Figure 5-D to F). Nevertheless, the underlying patterns of cross-correlation between migration, infanticide and birth remain nearly identical to those observed in a non-seasonal environment (Annex 3). Finally, as in non-seasonal environments, no synchrony is detected in patterns of infanticide.

III.4- Population level

At the population level, the increase in the level of reproductive synchrony with the introduction of infanticide is also detectable. Although the level of synchrony at the population level is much lower than at the troop level (mean $ac_{max}=0.062$, sd=0.005) (Figure 6), it is significantly stronger than the sychrony observed in the control (50 replicates: t=5.4, df=90.0, $p=10^{-6}$; 15 replicates: t=2.4, df=24.7, p=0.021).

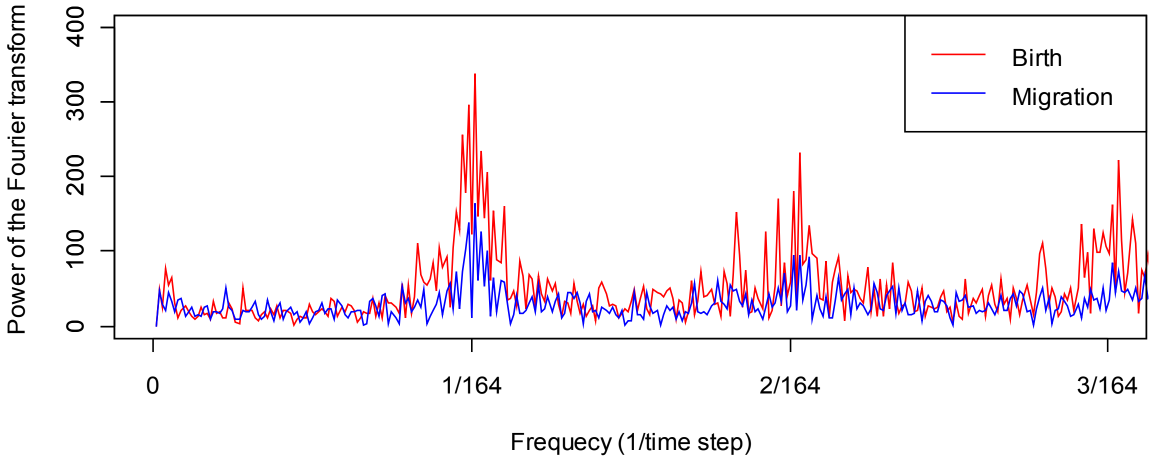

Figure 2: Spectrum of births (in red) and immigration (in blue) for one replicate. On both spectra, the clear peak at 1/164 shows the presence of synchrony with a period of the interbirth interval. The smaller peak for immigration indicates qualitatively that the synchrony in migration is weaker than in reproduction.

In male immigration, no particular pattern is observed at the population level, or the level of synchrony is too low to be significant. Similarly, once again, no pattern is detected with infanticide.

Nevertheless, patterns at the population level will be strongly influenced by patterns between troops. We might expect that if the troops are in perfect phase the birth synchrony at the population

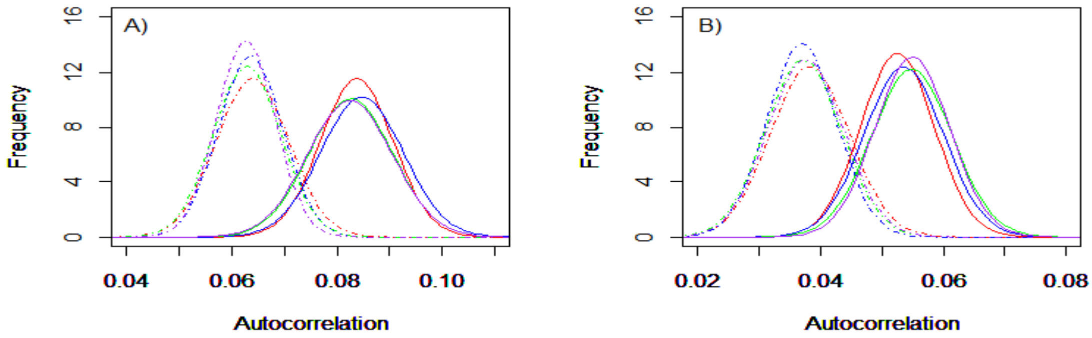

Figure 3: Distribution of the maximum autocorrelation values for simulations with and without infanticide, for births (A) and immigration (B). The colours represent the different troops in a population. In both cases, the dashed lines represent the control simulation without infanticide, the plain ones, the simulation with infanticide. The distributions are not significantly different from normality (Shapiro-Wilks tests: p>0.05 in all cases).

level will be higher than that observed at the troop level. In contrast, if the troops are in exact opposition of phase, no synchrony will be detected at the population level despite the existence of sychrony at the troop level. In our situation, we have observed a significant increase in reproductive synchrony despite the fact that there is no particular pattern of co-synchrony emerging between the troops. The cross-correlation functions (Annex 4) have no strongly significant peaks, and there is no apparent consistency between different pairs of troops. That means that all the troops seem to behave comparably, but the migration of males is not a strong link between them, such that the troops remain mostly independent.

The introduction of seasonality in the model radically changes this pattern. This is unsurprising, given that seasonality is a forcing at the population level. With increasing seasonal forcing, the different troops tend to synchronize together. When seasonality is sufficiently strong, all the troops are in phase with their females cycling together (Annex 5). As a result, with seasonality, increasing reproductive synchrony is detected at the population level (Figure 7). Moreover, only the significance of the annual period is increasing, while reproductive synchrony at the interbirth interval remains constant. For male immigration, seasonal forcing does not influence synchrony at the troop level. As a consequence, patterns at the population level are the same as those described earlier, without seasonality. Finally, once again, no pattern of sychrony is detected for infanticide.

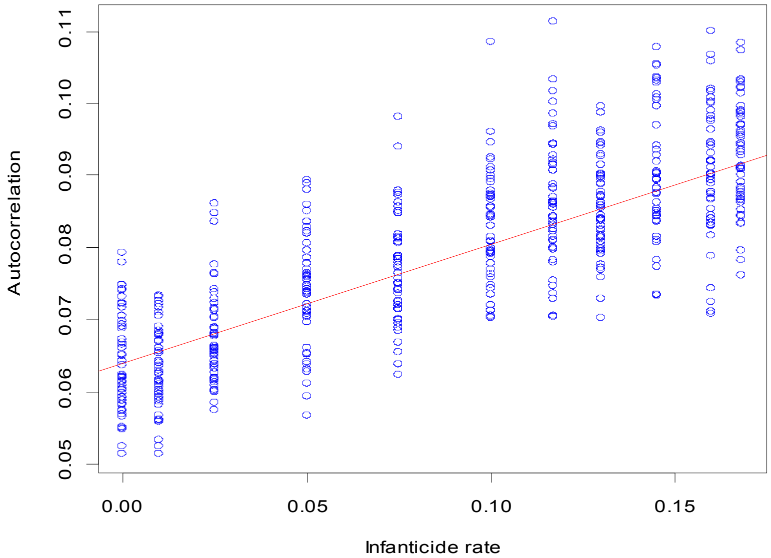

Figure 4: Effect of infanticide rate on reproductive synchrony. The blue points in column are the maxima of autocorrelation (ac_{max}) for the 50 replicates of one simulation with a given infanticide rate. The red line is the best-fit linear regression on the mean values: intercept = 0.064, slope = 0.16, adjusted R^2=0.92, F=93.1, df=1,7 and p=10^{-16}.

IV- Discussion

The findings of this study suggest that infanticide can have a significant effect on reproductive synchrony in a socially structured population. More precisely, infanticide increased the level of reproductive synchrony naturally present in social groups (in this case, baboon troops). In a non-seasonal environment, the synchrony in births was mostly detected at the troop level, and occurred with a period comparable to the interbirth interval. In each troop, male immigration followed reproduction (as females resumed cycling) and therefore also became synchronous at the interbirth interval. In contrast, infanticide never became synchronous. At the population level, a lower level of synchrony was detected in reproduction at the interbirth interval, and no pattern was detected in male immigration or infanticide. Moreover, without seasonality, the different troops in the

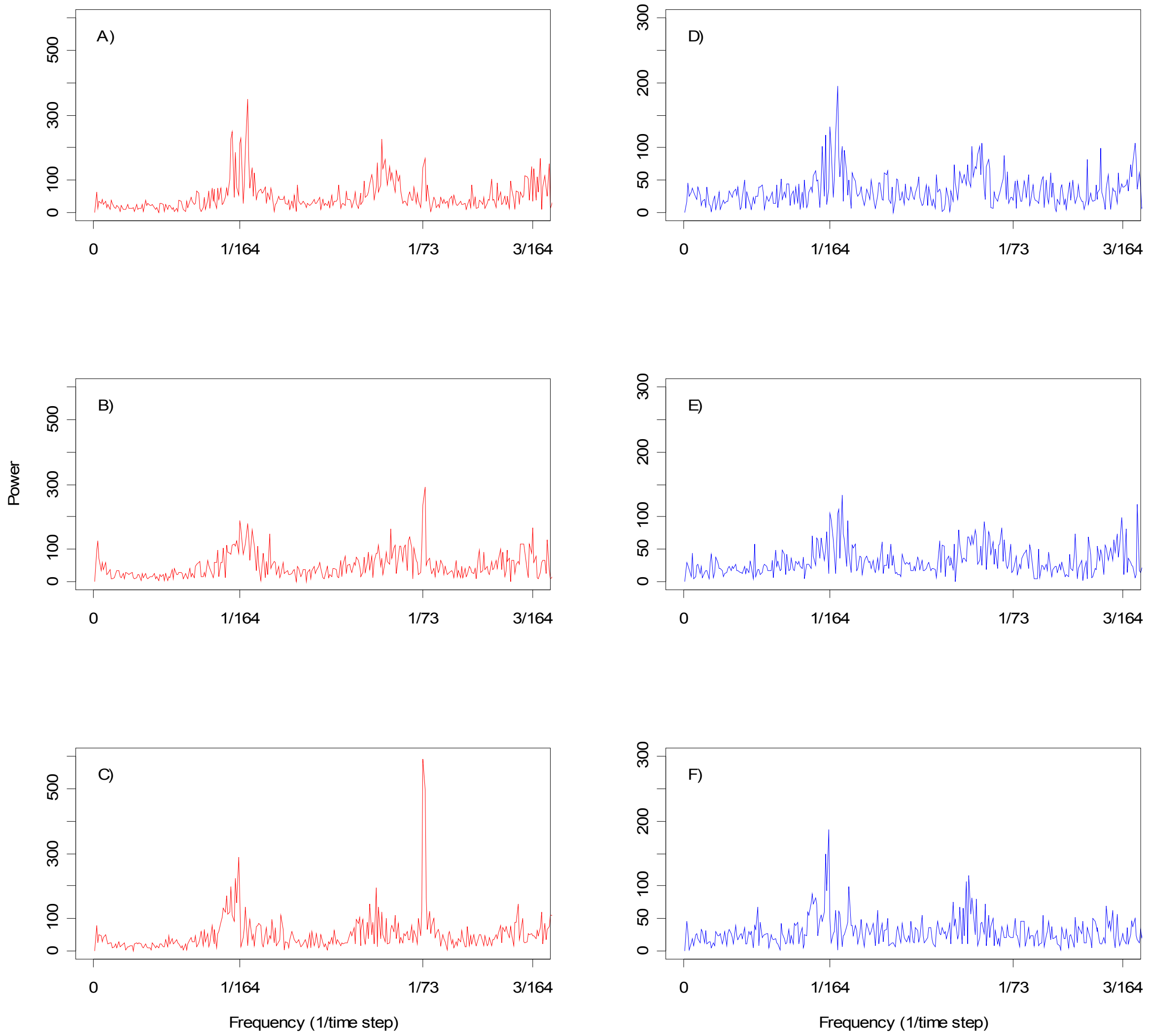

Figure 5: Effect of seasonality on reproductive synchrony (A to C) and synchrony on immigration (D to F). Each plot is the spectrum of time series for births (in red) and immigration (in blue) when seasonal forcing is weak (A and D), intermediate (B and E) and strong (C and F). With increasing seasonality, a peak at 1/73 (corresponding to a period of one year) appears in the births spectra but not the immigration spectra.

population remained mostly independent. When seasonality was added to the model, the annual period appeared as another significant period of synchrony in birth, but had no effect on immigration. At the population level, seasonality synchronized the troops together in phase. As a result, a very strong level of synchrony at the annual period was detected at the population level. However, migration remained unaffected by seasonality.

Our first finding was that when infanticide was added to the control simulation, reproductive synchrony increased significantly. Two key processes may have been responsible for this pattern. First, when an infanticide occurred, females that lost their infant resumed cycling more quickly than at the end of the lactation period (following Altmann & Alberts 2003). Second, and more importantly, those females resume cycling at the same time, and then tended to cycle synchronously. The emergent pattern of birth sychronisation from these processes was dependent on the rate of infanticide. Because of the stochastic processes in the model, if infanticide was rare, females tended to desynchronise. In contrast, when the infanticide rate increased, more females were affected by infanticide and put in phase at the same time. However, if infanticide was too frequent (with a higher rate than observed in reality and tested here in the model), we might expect that females would start to be interrupted in their reproductive cycle too often to maintain a high level of synchrony. Hence, although at each event of infanticide the females concerned would still resume cycling together, they would not stay in phase long enough to see any particular period of

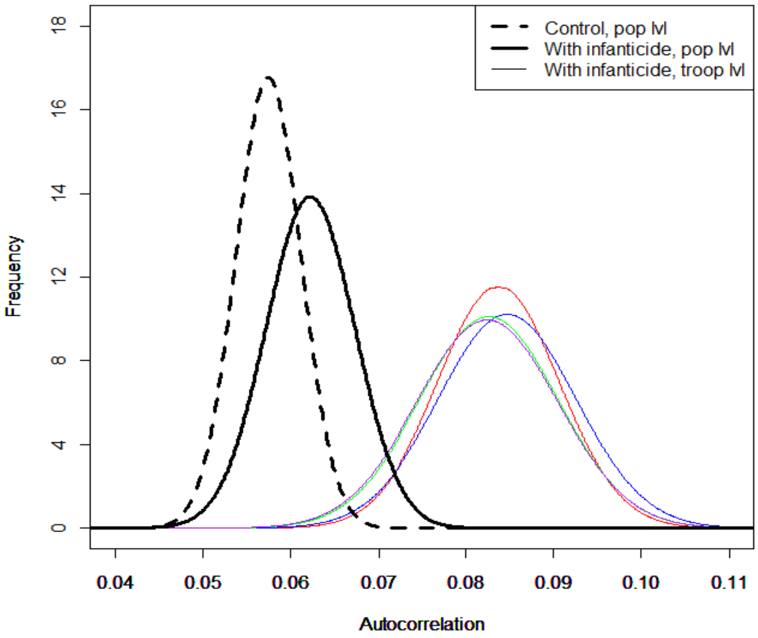

Figure 6: Distributions of the maximum autocorrelation values at the troop level with infanticide (thin colored lines), at the population level with infanticide (thick plain line), and at the population level in the control simulation (thick dashed line). The distributions are not significantly different from normality (Shapiro-Wilks tests: p>0.05 in all cases).

synchrony emerging. We could then expect a decrease in synchrony at the interbirth interval. Finally, if infanticide was extremely high, too many infants would be killed for adequate troop recruitment and the troop would not survive.

Under natural conditions, we observed that synchrony in male immigration also increased with infanticide. This can be explained by the fact that the migration of males was directly linked to the relative number of cycling females in the troop (following Alberts & Altmann 1995, Clarke et al. 2008), i.e. when females were in phase with each other, more females were cycling at the same time in the troop which made it more attractive to males. Contrarily, when the females were all pregnant or lactating, the attractiveness of the troop was very low, which caused emigration of males from the troop. Migration thus became synchronous with the rhythm of reproduction. One might further expect that if all females in a troop were in phase, and so too the migration of males, then males would have only entered the troop when all females were in oestrus, no infant would have been killed, and infanticide would have disappeared. However, migration was also dependent on the number of males present in the troop, which affected migration in the opposite way to the number of cycling females (following Alberts & Altmann 1995, Clarke et al. 2008). Indeed, if no females were cycling, the males inside would have tended to leave, and then the troop would have become more attractive to potential immigrants because of the low number of males present in it. These two opposite effects, combine with the fact that immigration events were rarer than birth events, explain in part why the level of synchrony in migration was lower than in reproduction. Moreover, different random processes (in the number of cycles before conceiving for example) and other processes (such as infant protection by the old alpha-male) acted to desynchronise females in a troop so that a situation where all females were strictly in phase with each other never happened and infanticide never disappeared.

Because infanticide was mostly committed by an immigrating male that has just entered the troop, we would have expect infanticide to have become synchronous as well. But infanticide never become synchronous in the situations tested. Two explanations could be given for this result. Firstly, male immigration did become synchronous, but the level of synchrony was very low, and may have been too low for infanticide to follow it and become synchronous as well. Secondly, infanticide remained a rare event, even compared to immigration. Infanticide could then have been too rare for any pattern of synchrony to be detected.

When seasonality was added to the model, the annual period also became significant in the pattern of reproductive synchrony. This was expected because seasonality directly affected the reproductive cycle of females through the probability of conception at the mating time. In contrast, male immigration did not follow the annual synchrony in reproduction. Although this is a counterintuitive result, it fits observations made in the field that male immigration in baboons is aseasonal

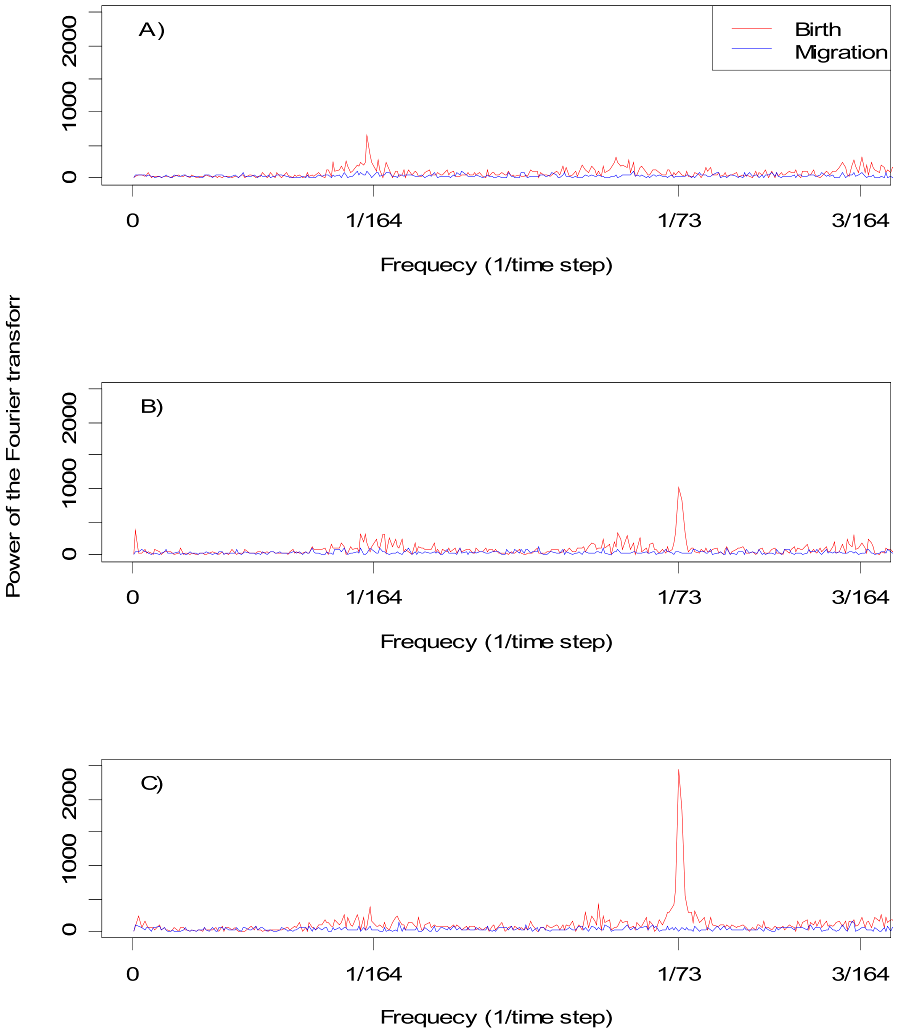

Figure 7: Spectra of births (in red) and immigration (in blue) for one replicate, at the population level, without seasonality (A), with intermediate seasonal forcing (B) and strong seasonal forcing (C). With increasing seasonality, we observe an increase of the peak at 1/73, because of the synchronization of the troops due to the seasonal forcing.

even where there is strong birth seasonality (e.g. Okavango, Botswana: Cheney et al. 2004). A possible explanation could be related to the finding that the interbirth interval remained the most significant period in reproduction even in a highly seasonal environment. Thus male immigration would have still synchronised in relation to reproduction, but only to the most significant period. However, this explanation needs further analysis of the model to be verified.

This study raises also more general questions concerning study of synchrony and individual-troop-population relations. Indeed, in studies of real troops of baboons, and more generally studies of birth patterns in groups of animals, the events of birth are generally recorded and plotted over a one-year plot (examples in Bentley-Condit & Smith 1997, Cheney et al. 2004, Brockman & van Schaik

2005b). Such a plot is very useful when the objective is to detect annual patterns in the distribution of births over time. However, as we have seen here, patterns of reproductive synchrony do not necessarily follow a period of one year. When seasonality is not considered, the main period of synchrony is the interbirth interval, which varies from one species to the other. In our case, the interbirth interval is 2.2 years. If this period was the only period of reproductive synchrony in a wild population, nothing would be detected on a one-year plot of births. Indeed, because the interbirth interval is not a multiple of one year, in successive years the peak of births would occur at progressively later dates. Over a long enough period of time, an annual summary would suggest that births are equally spread across the year. This suggests that in future studies of wild populations it would be useful to consider the possibility of birth synchrony with a different period to a year. This could be done most effectively by working on the whole time series rather than summarising monthly totals across the year, and using tools such as autocorrelograms or Fourier analyses to detect the significant periods.

Another interesting aspect of this study is how an individual behaviour can have a direct impact on the dynamics of the troop, and could even be detected by its influence on the whole population. Similar findings have also been found in previous individual-based models of population dynamics (Sumpter & Broomhead 2001, Ovaskainen & Hanski 2004). Infanticide is primarily an individual behaviour: the male chooses alone to commit infanticide, based on the situation of the troop in which he seizes alpha-male position. But his decision directly influences the reproductive cycle of the females in the troop, and consequently their birth distribution, and so finally juvenile recruitment to the troop, which in turn can directly affect the survival of the troop.

Further development of the model could bring to light other links between troops in a population. In particular, it would be interesting to investigate the influence of the size of the troops on the relationship between infanticide and reproductive synchrony. A first step would be to vary the size of the troops (keeping all troops the same size), to explore the extent to which the current results are sensitive to the size of troop. A second step would be to investigate how different sizes of troops within the same population could lead to the emergence of between-troop patterns, especially those that are independent of seasonality. Indeed, when males follow migration rules in which the natal troop is avoided, we might imagine that one bigger synchronous troop could directly influence a smaller troop. In other words, synchronous events in larger groups could drive patterns in smaller groups.

Finally, the model developed in this study should have wide generality. Although it has been explicitly parametrised for baboons, the model design is sufficiently general to fit a variety of species where infanticide is present. The model results discussed here could easily be explored using parameters derived from other species that might include not only other primates, such as hanuman langurs (*Semnopitheaus entellus*), red howlers (*Alouatta seniculus*), and Thomas' langurs (*Presbytis thomasi*)... (van Schaik & Janson 2000), but also others mammals - especially rodents (Blumstein 2000) and carnivores, such as lions (*Panthera leo*) (Packer & Pusey 1983) - and even birds (Veiga 2000). That would allow us to generate very general results on the behavioural ecology of infanticide and its impact on the individual and on wider population dynamics.

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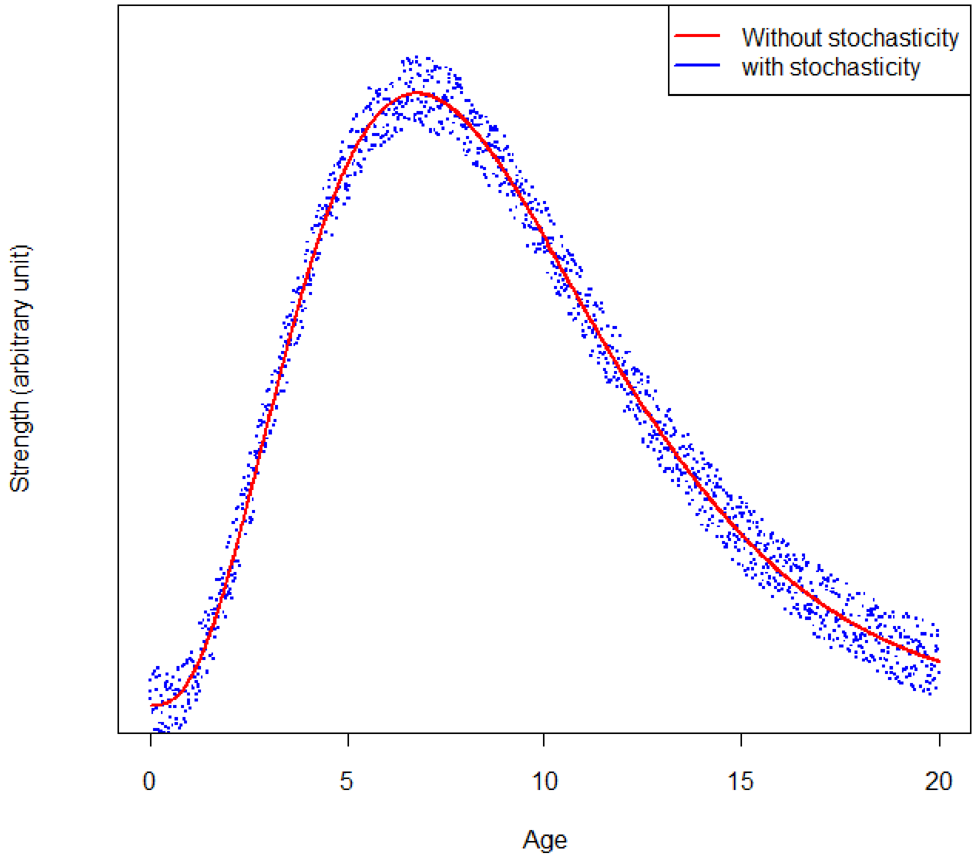
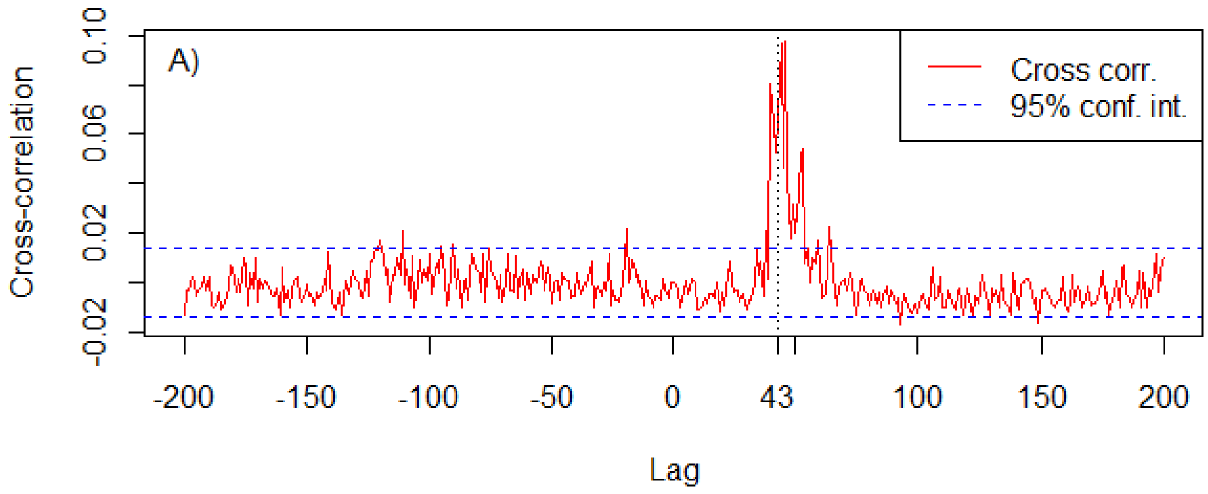
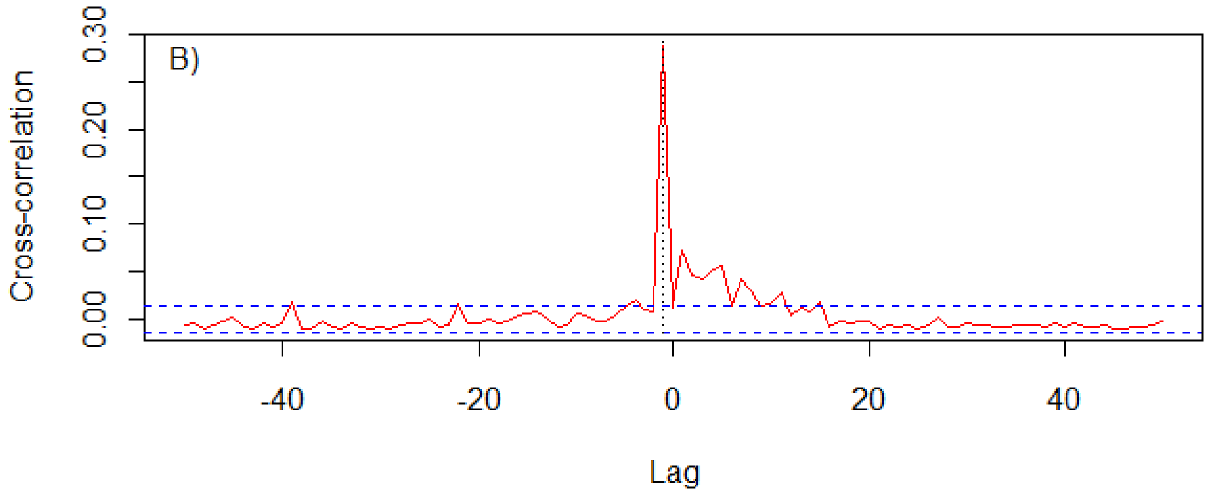
V- Annexes

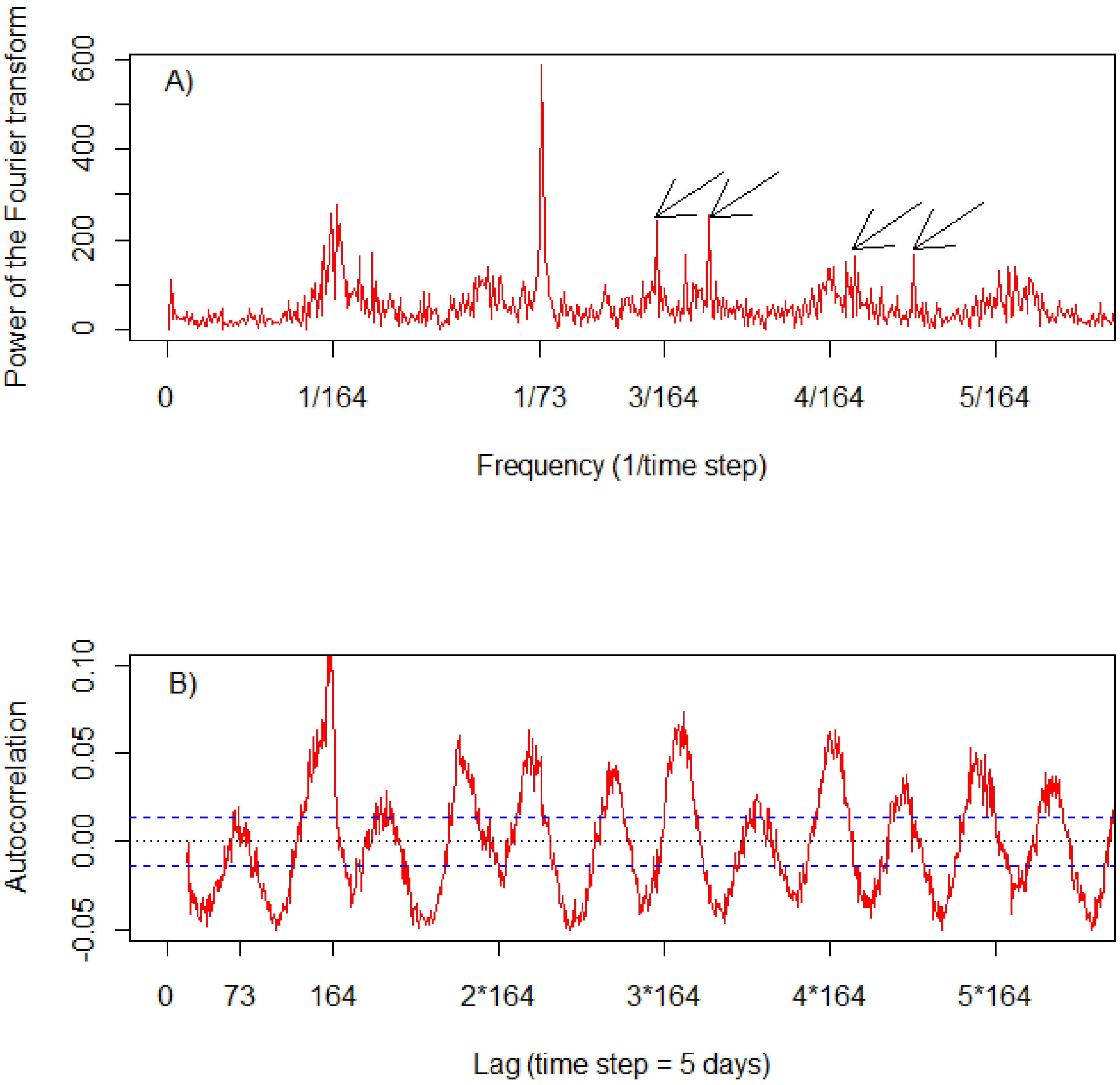


Annex 1: Relation between age and strength. The maximum of strength occurs around 7 years of age.

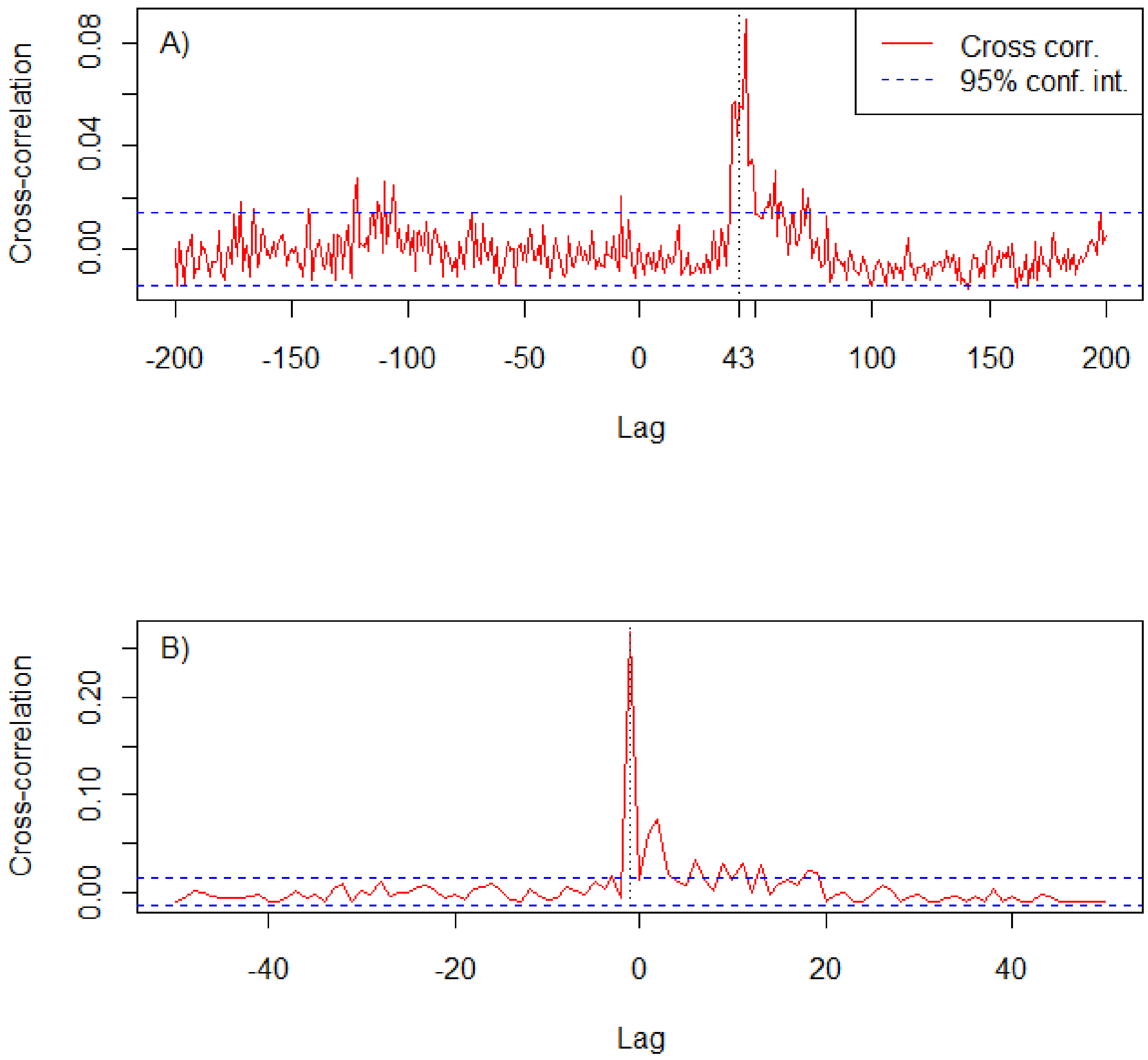




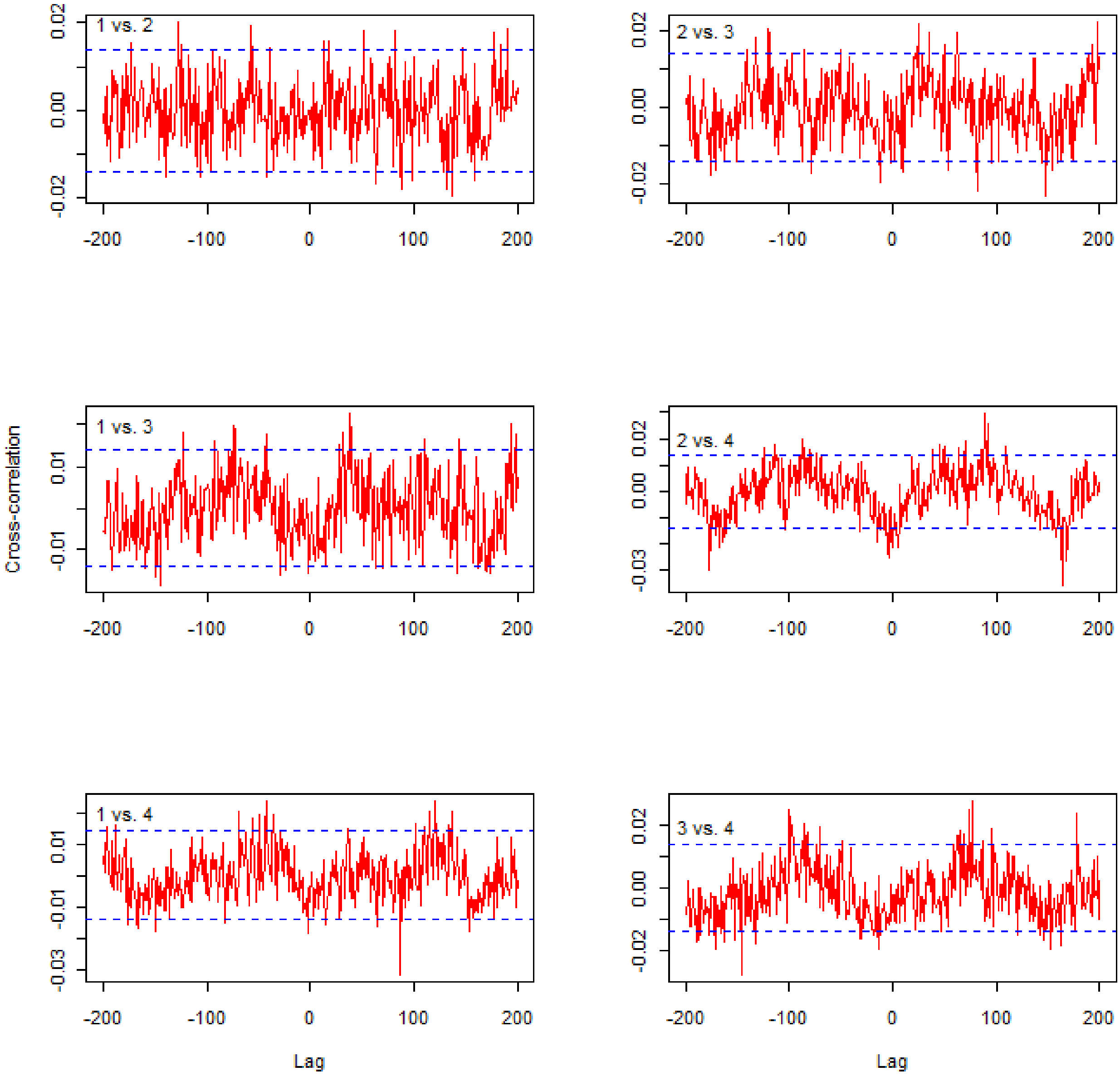
Annex 2: Cross correlation of infanticide versus birth (A) and infanticide versus immigration (B) at the group level in a non seasonal environment. The peaks on the cross correlograms show the presence of a particularly significant lag between two time series tested. Plot (A) shows that infanticides are generally followed by births 43 time steps later. Plot (B) shows that infanticide is almost always preceded by an immigration. The blue lines represent the 95% confidence interval, as on an autocorrelogram.



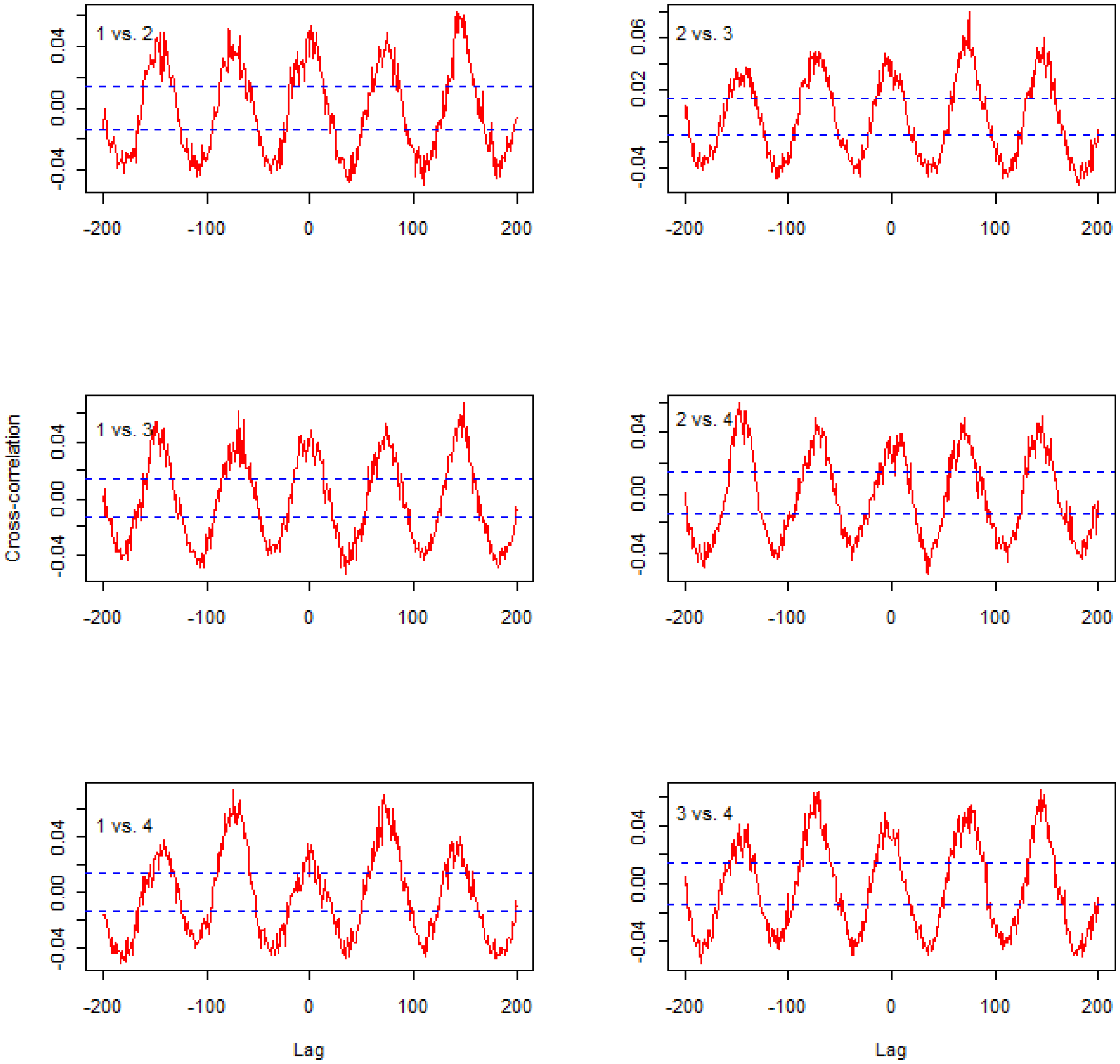
Annex 3: (A) Spectrum of births in a highly seasonal environment. This spectrum shows the presence of the two main frequencies, the interbirth interval (1/164) and the seasonality (1/73), but also new peaks that could possibly correspond to interference between those two main frequencies (arrows). (B) Autocorrelogram corresponding to the spectrum. The peaks at the annual period and the interbirth interval show the presence of those two periods in the signal. But the peaks at a multiple of the interbirth interval have changed compared to a non seasonal environment (compare with Figure 1-C). The more complex pattern shown on this autocorrelogram seems to confirm the hypothesis of interference raised by the spectrum. The blue lines represent the 95% confidence intervals.



Annex 4: Cross correlation of infanticide versus birth (A) and infanticide versus immigration (B) at the group level in a seasonal environment. Plot (A) shows that infanticide events are again generally followed by births 43 time steps later. Plot (B) shows that infanticide is again almost always preceded by an immigration. Thus seasonality does not appear to affect the cross correlation between infanticide, migration and birth (compare with Annex 2). The blue lines represent the 95% confidence interval.



Annex 5: Cross correlation of births between the different troops two-by-two in a non-seasonal environment. Either no pattern or very weak patterns are present between the troops. When a weak pattern does appear within a pair there is no apparent consistency with other pairs. Thus no clear pattern of synchrony exists between the four troops of the population. The blue lines represent the 95% confidence interval.



Annex 6: Cross correlation of births between the different troops two-by-two in a highly seasonal environment. Comparison of the six cross correlograms shows that a clear pattern of synchrony emerges between the troops in a seasonal environment, with all the troops being synchronized in phase. The blue lines represent the 95% confidence interval.

Ims 1990Darling 1938Brockman & van Schaik 2005avan Schaik & Janson 2000Janson & Verdolin 2005Judson 1994Grimm 1999Collinset al. 1984Palombit et al. 2000Henzi & Barett 2003Altmann & Alberts 2003Alberts & Altmann 1995Alberts et al. 2003Cheney et al. 2004Clarke et al. 2008Bentley-Condit & Smith 1997Brockman & van Schaik 2005bPacker & Pusey 1983