I- Introduction

Reproductive synchrony characterizes the tendency in certain species to achieve particular phases of the reproductive cycle, such as birth, at the same time as other members of the population they belong to. It is a very common phenomenon that has been documented for a large variety of living organisms, from plants to animals, such as birds, mammalian or even humans. Synchronizing reproduction can have different interests for the individuals. First, it has been described as a process involved in avoiding predation for a long time [Darling1938], [Ims1990]. Indeed, if many adults are breeding at the same time, it increases the protection of the offspring by increasing the number of adults involved in collective defence. Moreover, by increasing the number of offspring present at the same time in a population, the probability for each infant to be killed by predation is reduced, this is called the dilution effect. But predation avoidance is not the only common reason given to explain reproductive synchrony. Seasonality is also recognized as a strong factor that leads to reproductive synchrony. Indeed, Breeding according to the seasonal environment can help to minimize the energetic cost of reproduction, for example by synchronizing birth with the period when foraging is easy [Brockman2005a].

Particularly in the case of synchrony caused by the environment, reproductive synchrony is occurring within populations. However, in socially structured species, reproductive synchrony can be more complex with possible synchrony within groups, but not between groups (at the population level). This is particularly relevant in the case of a lot of primate species, where the social organisation leads to populations with spatially differentiated groups with their own social structure. Interesting pattern can then emerge with temporal organisation of birth that would provoke reproductive synchrony within a group, and could then affect the dynamic of the whole population, causing emergence of pattern between the groups. This is a good example of how a group based pattern can have an effect on the population.

In a group, seasonality is not the only explanation to the emergence of reproductive synchrony. Indeed, some individual based behaviours are supposed to be the origin of reproductive synchrony. One of those behaviours is the infanticide. An infanticide is the event when a mature animal kills a young offspring of its own species in purpose. In social species living in groups, and particularly polygynous species, infanticide is generally committed by a male that has just arrived in the troop, to have a chance to get his own offspring. Infanticide in mammals has been well documented among primates [Schaik2000], which then constitute a good example for the study of its implication in reproductive synchrony.

The study presented here consider a theoretical approach of the role to infanticide in reproductive synchrony by trying to model the dynamic of a group and a population in a social species facing infanticide. The approach used here is an individual-based model. With increase of computational power, individual-based model have been more and more widely used in ecology [Judson1994] [Grimm1999]. This approach allows to characterize precisely each individual represented in the model and its role, and observe results at all the different levels, from the individual to the group, the population, and even the metapopulation. This is then a very powerful tool to study the impact of an individual based behaviour, such as infanticide, on a group or a population dynamic.

Because infanticide has been very well documented on primate, and especially baboons, we have used the baboons has a case study. We have used an individual-based modelling approach to examine the effect of infanticide on reproductive synchrony in a artificial baboon population. Our objectives are to demonstrate that infanticide is a key behaviour in producing reproductive synchrony, in different environments. More precisely, we have first investigated the role of infanticide in synchronizing birth and other processes related to it, such as migration of males, in a non seasonal environment. Then, we have studied the impact of a seasonal environment, with different level of seasonality, in interaction with infanticide, on synchrony in reproduction and migration. In both cases, the effect of infanticide and seasonality (when present) has been considered both within groups, and between groups in a population of four groups, to look for the emergence of patterns at the population level.

II- Model implementation and methods

II.1- Model design

We built a discreet time model where each individual is represented explicitly. This individual based model aims at creating a population of baboons to investigate the effect of infanticide on synchrony in reproduction and other related processes. A population is composed of several independent troops, 4 in the model, related by the migration of males between the troops. A group is composed of three different classes of individuals, resident females and immatures, and males coming and leaving through migration. In each class, an individual is represented by its age and a state. The different possible states depend on the class of individual. A female can be in four different states, describing a simplified reproductive cycle:

- Cycling: with a duration of 35 days, this state corresponds to the menstrual cycle of a baboon.

- Mating: during the menstrual cycle, at the oestrus, the female can copulate if a male is present in the group. This event is considered to be instant, but determine the rest of the cycle. If the female does not conceive, she finishes her menstrual cycle normally. On the other hand, if she conceives, the menstrual 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 enter the lactating state.
- Lactating: this state lasts 18 months. At the end of the lactating period, the infant is weaned, and the female resume cycling within a variable period of time depending on random processes.

In all the different states, adult females have the same probability of death at each step.

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

- Infant: an infant is an immature before weaning. This state correspond to the lactating state of the mother and lasts 18 months.
- Juvenile: after weaning, an immature is called juvenile until it reaches maturity. The time needed to reach maturity depends on the sex of the juvenile, and the size of the group by density dependence processes that promote early recruitment as a mature individual in a low density troop [Altmann2003].

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. When an immature reaches maturity, it is recruited depending on the sex. Females are directly recruited to the natal group. Males always leave the group and are recruited to an external pool of males from where they will migrate to another troop, as explained later.

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

- Outside a group: the male is then considered as a solitary male that can immigrate in a group. In the model, all the solitary males are modelled in the same external pool of males, but are all behaving independently.
- Subordinate in a group. In that state, the male has the possibility to leave the troop, or to try to take over the dominant position.

- Dominant in a group. At any time in a troop, only one male can be dominant. Despite the extreme case of no male being present in troop, the group can't be left without a dominant

Migration is an important process in the model that can lead to 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 migration to a troop or from the troop depends on the attractiveness of the troop, which depends on the number of cycling female per male present. 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 can only go into the external pool before having the possibility to go anywhere else, as migration can't be direct from one troop to another. When a male enters a troop, he enters as a subordinate and can either stay subordinate, or challenge the dominant to try to take over the dominant position.

A challenge is provoked by a subordinate, called the challenger. The challenger can either be a resident subordinate or one that has just arrived through migration. The possibility of challenge occurring is directly dependent on the respective ages of the dominant and the challenger, the age determining the strength of the individual, and the origin of the challenger, one that has just arrived being much more likely to challenge the dominant compared to a resident of the same strength. A subordinate will challenge the dominant if he is strong enough compared to the dominant. The result of the challenge depend also on the strength of the contestants, and random processes. The looser of the challenge has the possibility to stay in the troop as a subordinate. If a challenger takes over the dominant position, he has then a probability to commit infanticide.

During an event of infanticide, the new dominant tries to kill all the infants, and the ex-dominant can stay in the troop and try to protect the infants. If an infant is killed, the mother resumes cycling in a shorter period of time than at the usual end of the lactation period. 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.

The different parameters that rule 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 4 troops. The initial composition of each troop is 20 females with a random state and age, as many infants as lactating females, no juveniles, 1 dominant and one subordinate male with a random age; the ages and states are picked in a uniform distribution. The time step is set at 5 days, and one simulation covers a period of 20000 time steps (274 years).

	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	[Cheney 2004]
Infants	0,17	[Cheney 2004]
	Other parameters	
Probability of infanticide		
male from the inside	0,05	-
immigrating male	0,8	-
Probability for the ex-dominant to stay		
Probability of protection by the ex-dominant		
against male from the inside	0,75	-
against immigrating male	0,8	-
Percentage of infant protected	0,5	-
Probability of conception	fix: 0.5, seasonal: 0.5 - [0:1]	-
Probability of immigration	$p \propto (1+f_{cycling})/(1+m_{inside}+f_{cycling})$	
Probability of emigartion	$p \propto (1+m_{inside})/(1+m_{inside}+f_{cycling})$	

Table 1: Parameters used in the model. 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.*

Different situation are modelled using those rules. The first one is a control simulation with no infanticide nor seasonal forcing. The second situation has still no seasonality, but the males can commit infanticide. In the last situation, a seasonal forcing is added to the probability of conception of a female at the mating time. The seasonal forcing is a simple cosine function with a period of one year and a variable amplitude that allows to vary this probability of conception of females from a fixed value to a function going from 0 to 1 depending on the time in the year.

II.2- Methods for analysing the results

In order to validate the model we have recorded the number of individuals in each class in each troop all along the simulation to get information on the dynamics of the troops, and statistics on the general behaviour of the model such as migration rates, tenure length, number of challenges and take overs, number of event of birth and infanticide rates. During a simulation, the number of births, infants killed and immigrating males is recorded in each troop at each step. This produces times series (Figure 1-A) that are analysed to look for synchrony in reproduction, infanticide and migration.

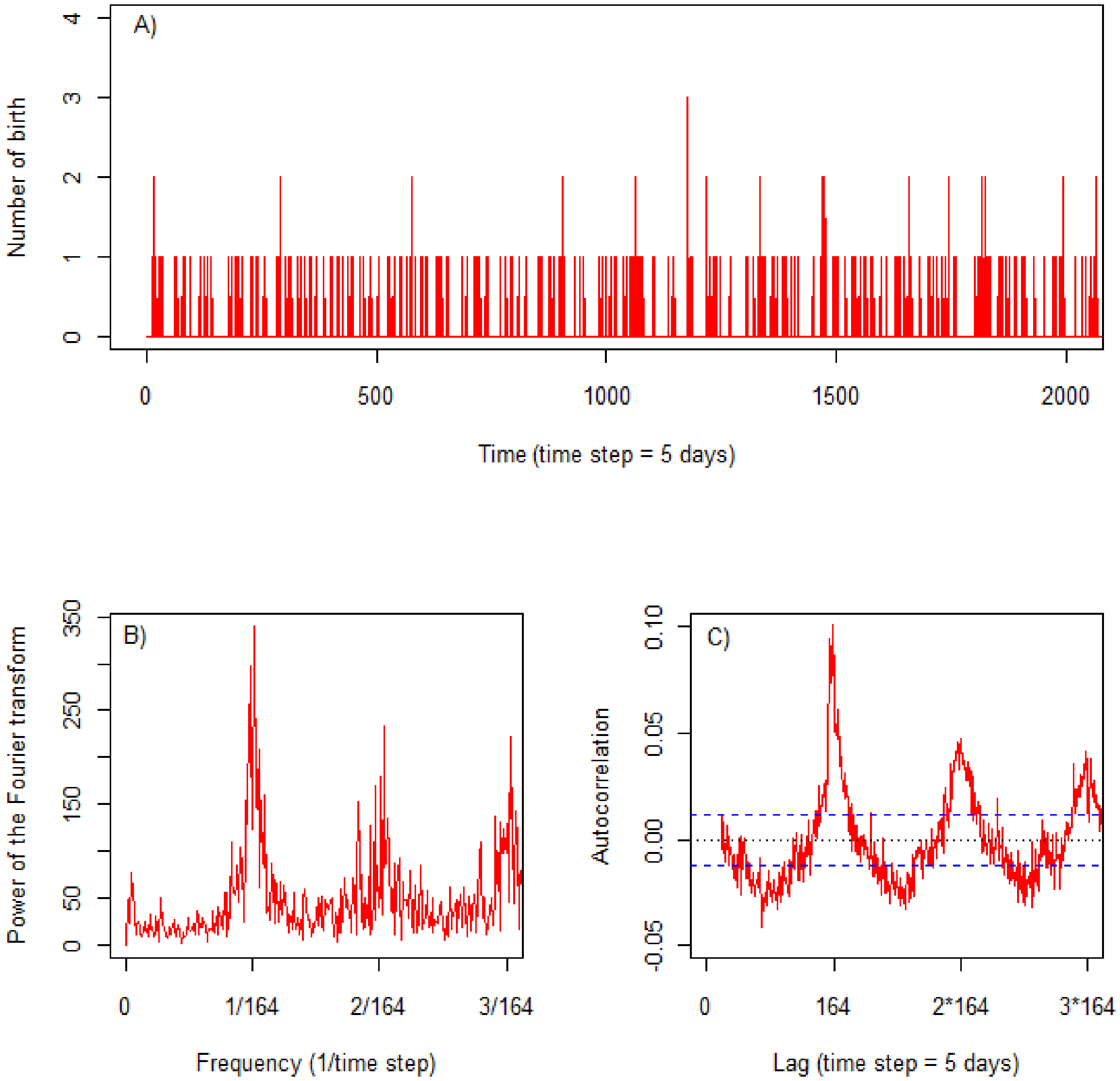


Figure 1: A) Extract of a time series for births. Each peak represent an event of one or several births at the same time. B) Spectrum of the time series. Higher frequencies are not shown because only the noise is present. The first interesting peak, at 1/164, corresponding to the interbirth interval, 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.

Different methods are used to analyse those time series and detect the presence of synchrony. The spectrum of a time series is given by a Fourier analyses. The spectrum of a time series gives information on the presence of one or several dominant frequencies in the time series (Figure 1-B). The Fourier analyses is a very powerful way of determining precisely the main frequencies present in a signal, by reading the spectrum and locating the peaks.

But the significance of those frequencies is given by the area under the peaks, which is not easy to measure on a spectrum. To determine the importance of a frequency in a time series, we have used the autocorrelation function (Figure 1-C). The autocorrelation is less precise in determining the main frequencies, particularly when several frequencies interfere together, but allows to measure easily the significance of a period when it is the only one present in the signal.

To determine the presence of synchrony in a time series we have then used the Fourier analyses. When only one frequency was significant on the spectrum, we have used the autocorrelation function to measure the significance of that frequency. A peak in autocorrelation is significant when it is above the 95% confidence interval. Because of the stochasticity introduced in the model, to have some statistical robustness in our results, one simulation consists of 50 replicates with the same parameters. The maximum value of autocorrelation at the frequency detected in each time series has been measured (Figure 1-C). For each time series studied (reproduction, infanticide and migration), we analysed the distribution of that maximum value of autocorrelation (referred to hereafter as the distribution of autocorrelation) to determine the level of synchrony. To study the effect of infanticide on reproductive synchrony and other synchrony derived from it, we first use a Shapiro test of normality to verify that all the distributions are normally distributed. Then we compared the distribution of the maximum of autocorrelation with infanticide to a control with the same parameters but no infanticide, using a t-test without assumption of equal variance. Because the result of a t-test can be highly dependent on the sample size, we used a smaller sample size of 15 replicates by selecting randomly some of the replicates for each distribution.

With the addition of seasonality, the signal becomes 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 impact of the different frequencies in the signal.

To study patterns of synchrony between troops, we compared the time series using the cross-correlation function. 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 are summed to get time series for reproduction, infanticide and migration. On those three new time series, synchrony is studied as described above.

III- Results

III.1- Model validation

To validate the model, we aimed at having a population that behaves in a comparable way to real populations, in terms of population size, migration rates, replacement rate of the dominant, etc. The control simulation is used to validate the parameters and set the default values of the different key statistics. The density dependence added to the model is set to help having stable troops. In reality, troops and populations are not necessarily stable. Growing troops can exist and split in two when they reach their limit of sustainable size. For reasons of simplicity in programming, we have chosen to stick with stable troops and stable populations. When a troop reaches the steady state, it is composed of 17 to 22 females, 3 to 8 males and around 30 to 35 immatures, to fit a generic composition [Cheney2004]. The other parameters and statistics used to validate the model are summarized in Table 2.

	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]
Number of challenges / yr	m = 0.60, sd = 0.045		-	
Number of take overs / yr	m = 0.35, sd = 0.026		-	
Number of birth / yr	m = 9, sd = 0.4		-	

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

Without infanticide in the model, a low level of synchrony is still present due to the fact that with around 20 females in a troop and stochasticity, some female may cycle in phase by chance. The level of synchrony is given by the distribution of the maximum of autocorrelation, as explained earlier. In this case, the distribution fit the normal distribution N(m=0.064,sd=0.006) (Shapiro-Wilk test: W=0.97, n=50, $p_{value} = 0{,}34$). The synchrony in reproduction occurs with a period of 164 time steps (around 2.2 years), which correspond to the interbirth interval, the average time separating two consecutive births. With these conditions, considering the autocorrelograms of the migration time series, a very low level of synchrony seems also to be present in immigration of males: the distribution of autocorrelation fits the normal distribution N(m=0.038,sd=0.006) (Shapiro-Wilk test: W=0.97, n=50, $p_{value} = 0{,}33$). Finally, no synchrony at all is present in infanticide, and no particular pattern exists between troops. All the troops are behaving independently, a low level of reproductive synchrony is still detectable at the population level, but lower than the one for each group separately (the distribution of autocorrelation follows the normal distribution N(m=0.057,sd=0.004)) (Shapiro-Wilk test: W=0.97, n=50, $p_{value}=0{,}22$), and no synchrony is present in migration at the population level.

When infanticide is added, parameters in the model such as the probability of infanticide when there is a take over or the probability for the ex-dominant to protect some infants, are set so that the infanticide fits values measured in the field (Table 1 & 2). With infanticide in the model, the troop sizes and the other parameters and statistics remain comparable (with possible variation due to stochasticity).

III.2- The effect of infanticide at the group level

The first important results of the model on the effect of infanticide on reproductive synchrony and other related patterns concern the group level. With the addition of infanticide to the model, we observed several changes compared to the control simulation.

First of all, with infanticide, we observed the presence of a significant frequency in the time series of birth corresponding to the interbirth interval, as in the control (Figure 2). Moreover, as shown on Figure 3-A, the distributions of autocorrelation at the interbirth interval for the 4 troops in the same simulation are very similar. For the different distributions, all the measures of autocorrelation are normally distributed (for example, the distribution of autocorrelation for troop 1 fits the normal distribution N(m=0.084,sd=0.006), Shapiro-Wilk test: W=0.98, n=50, $p_{value}=0{,}634$). In addition, the distributions of the autocorrelation for the 4 troops in the control simulation and the simulation with infanticide are very different (Figure 3-A). The result of the t-test is very significant with the

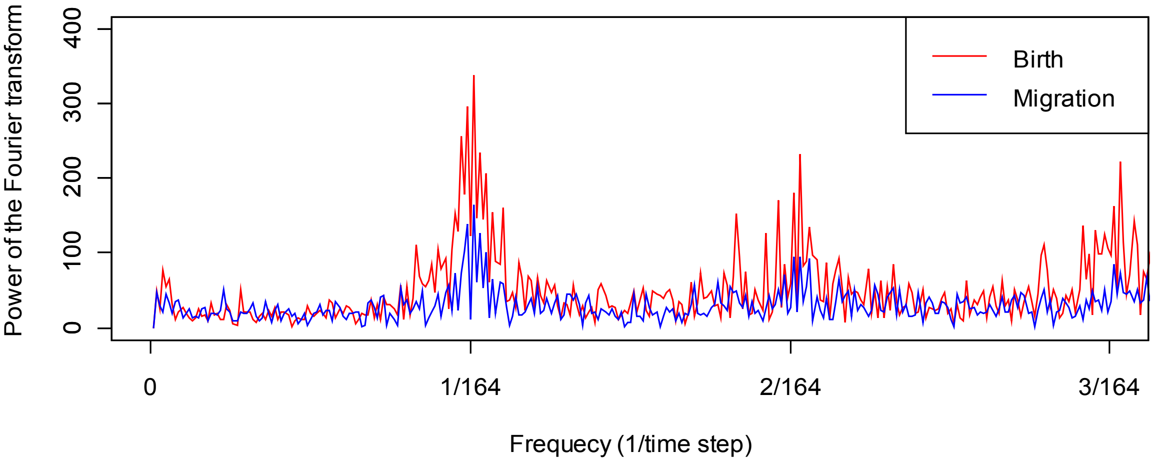


Figure 2: Spectrum of birth (in red) and migration (in blue) for one replicate. On both spectra, the clear peak at 1/164 shows the presence of synchrony with a period of the interbirth interval. The smaller peak for migration indicates qualitatively that synchrony in migration is weaker than in reproduction.

two different sample sizes used: with 50 replicates: t=15.5, df=96.3, $p_{value} < 10^{-16}$, with 15 replicates: t=9.4, df=27.5, $p_{value} < 10^{-10}$, which means that this result is robust to variation in the sample size. Infanticide has therefore a significant effect in increasing the reproductive synchrony in a troop of baboons.

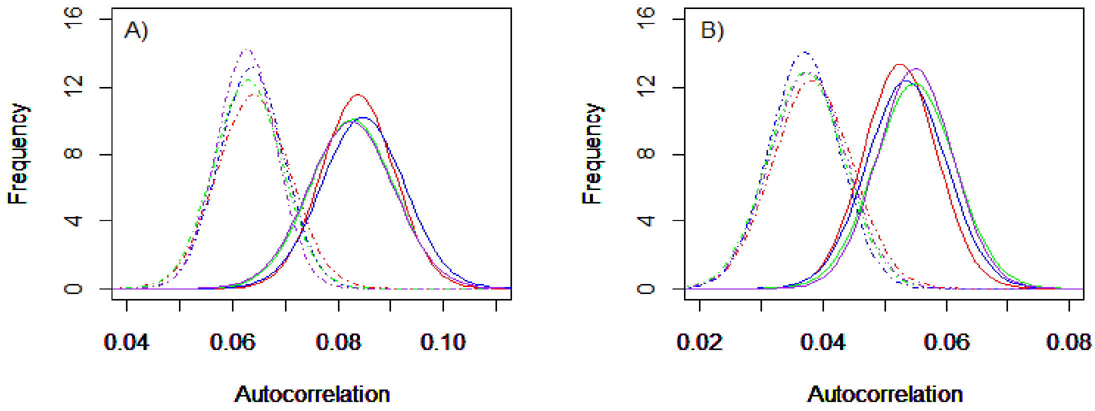


Figure 3: Distribution of autocorrelation for simulations without and with infanticide, for birth (A) and migration (B). The colours represent the different troops in a population. In both cases, the dashed lines represent the control simulation without infanticide, the plain ones, the simulation with infanticide.

With the synchronization of the females, we observed some synchronization of male migration in all the different troops at the interbirth interval (Figure 2 and 3-B). Once again, for the same simulation in the different troops, the distributions of autocorrelation are very similar and all the measures of autocorrelation are normally distributed (for example, the distribution of autocorrelation for troop 1 fits the normal distribution N(m=0.052,sd=0.006), Shapiro-Wilk test: W=0.98, n=50, $p_{value} = 0{,}7536$). We observed also an increase in this synchrony compared to the control. Indeed, the distributions of autocorrelation in the different troops for the simulation with infanticide is significantly different from the control: with 50 replicates t=12.6, df=97.8, $p_{value} < 10^{-16}$, with 15 replicates t=6.3, df=26.8, $p_{value} < 10^{-6}$. Infanticide seems then to increase significantly the synchrony in migration as well as in reproduction.

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

As infanticide increases the reproductive synchrony, we studied the effect of the infanticide rate on the level of synchrony. We explore a large range of infanticide rates, from 0% (control situation) to nearly 17%, all other parameters remaining unchanged. As it could be expected, the rate of infanticide has a direct effect on the level of synchrony, measured by the maximum value of autocorrelation (Figure 4). Moreover, a linear regression gives the following best fitted line: $\text{Autocorrelation} = 0.063 + 0.18\ \text{Infanticide rate}$, with the $p_{value} < 10^{-16}$ for the slope and the intercept, and more than 90% of the variance explained.

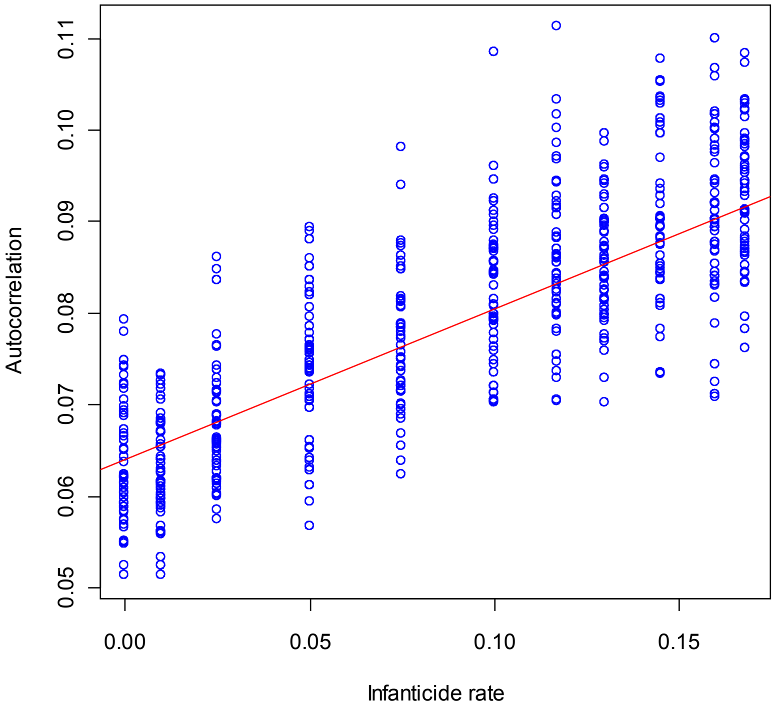


Figure 4: Effect of infanticide rate on reproductive synchrony. The blue points in column are the maxima of autocorrelation for the 50 replicates of one simulation with a given infanticide rate. The red line is the best fitted line on the mean values, intercept = 0.064, slope = 0.16 and adjusted R-squared=0.92, F=93.1, df=1,7 and $p_{value} < 10^{-16}$.

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. As we can see on the spectra (Figure 5-A to C), for the whole range of seasonality we have tested, the period of the interbirth interval remains present in the time series, and a qualitative comparison of the area under the peaks of interbirth interval and seasonality suggests that the interbirth interval remains the most significant period that explains the signal. However, although the limit is difficult to find clearly, when seasonal forcing is strong enough, we observed other small peaks on the spectrum than the ones corresponding to the interbirth interval and seasonality (*cf.* Annex 2). Those new peaks could suggest the existence of interference between the two dominant frequencies in the time series. The complexity of the corresponding autocorrelogram (*cf.* Annex 2) tends to confirm this hypothesis. In conclusion, independently of complex interference, with seasonality in the model we have coexistence of two periods of synchronization of reproduction, the interbirth interval and the year, giving a more complex time series than before.

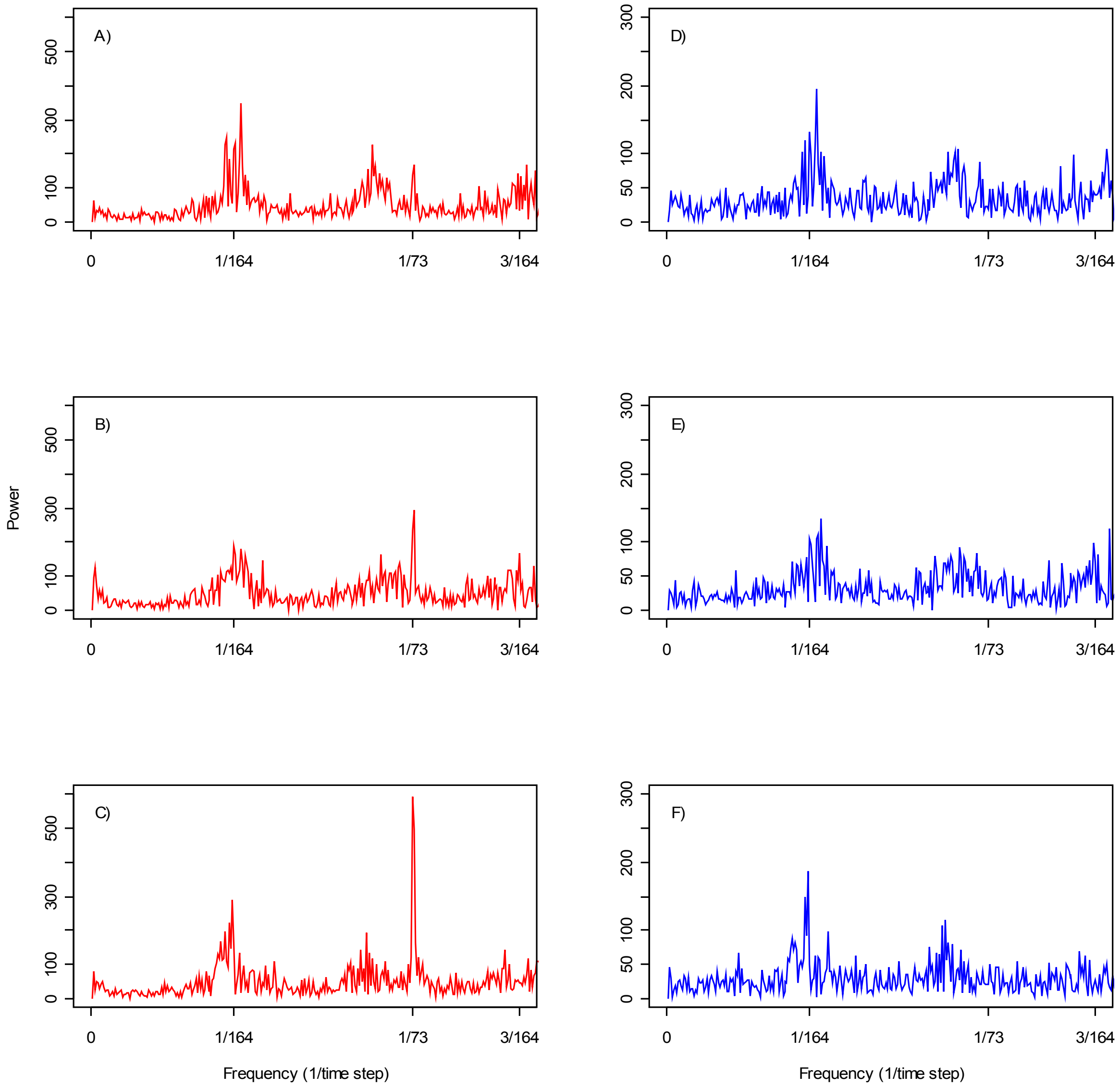


Figure 5: Effect of seasonality on reproductive synchrony (A to C) and synchrony on migration (D to F). Each plot is the spectrum of time series of birth (in red) and migration (in blue) for a weak seasonal forcing (A and D), a middle one (B and E) and a strong one (C and F). With increasing seasonality,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

Unexpectedly, migration does not follow the reproduction rhythm. Although migration is directly related to the female cycle through the attractiveness of the troop, the seasonal forcing has absolutely no effect on migration. For the whole range of seasonality, migration only synchronizes at the interbirth interval (Figure 5-D to F). Patterns of cross-correlation between migration, infanticide and birth remain nearly identical (*cf.* Annex 3). Finally, as without seasonality, no synchrony is detected in infanticide.

III.3- Population level

At the population level, the increase in the level of reproductive synchrony is also detectable. Although the level of synchrony at the population level is much lower than at the troop level (the distribution of autocorrelation follows the normal distribution N(m=0.062,sd=0.005), Shapiro-Wilk test: W=0.98, n=50, $p_{value}=0.74$) (Figure 6), the distribution of autocorrelation is still significantly different from the control: with 50 replicates t=5.4, df=90.0, $p_{value}<10^{-6}$, with 15 replicates t=2.4, df=24.7, $p_{value}=0.021$. In migration, no particular pattern is observed at the population level, or the level of synchrony is too low to be significant. Once again, no pattern is detected concerning infanticide.

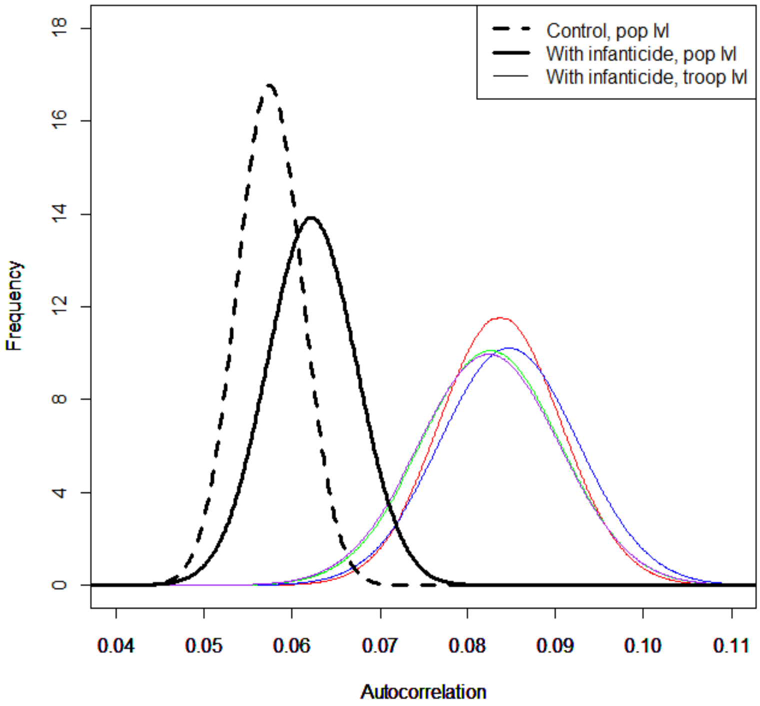


Figure 6: Distributions of autocorrelation at the troop level with infanticide (thin colored lines), at the population level with infanticide (thick plain line) and at the population level in the control simulation (thick dashed line).

But patterns at the population level are very influenced by patterns between troops. Indeed, if the troops are in phase, the synchrony at the population level will be higher, whereas if the troop are in exact opposition of phase, no synchrony will be detected at the population level although there is some at the troop level. In our situation, no particular pattern is emerging between the troops. The cross-correlation function (*cf.* Annex 4) has no really significant peak, and especially nothing particularly reproducible. That means that all the troops seem to behave comparably, but the migration of males is not a strong link between them, and they remain mostly independent.

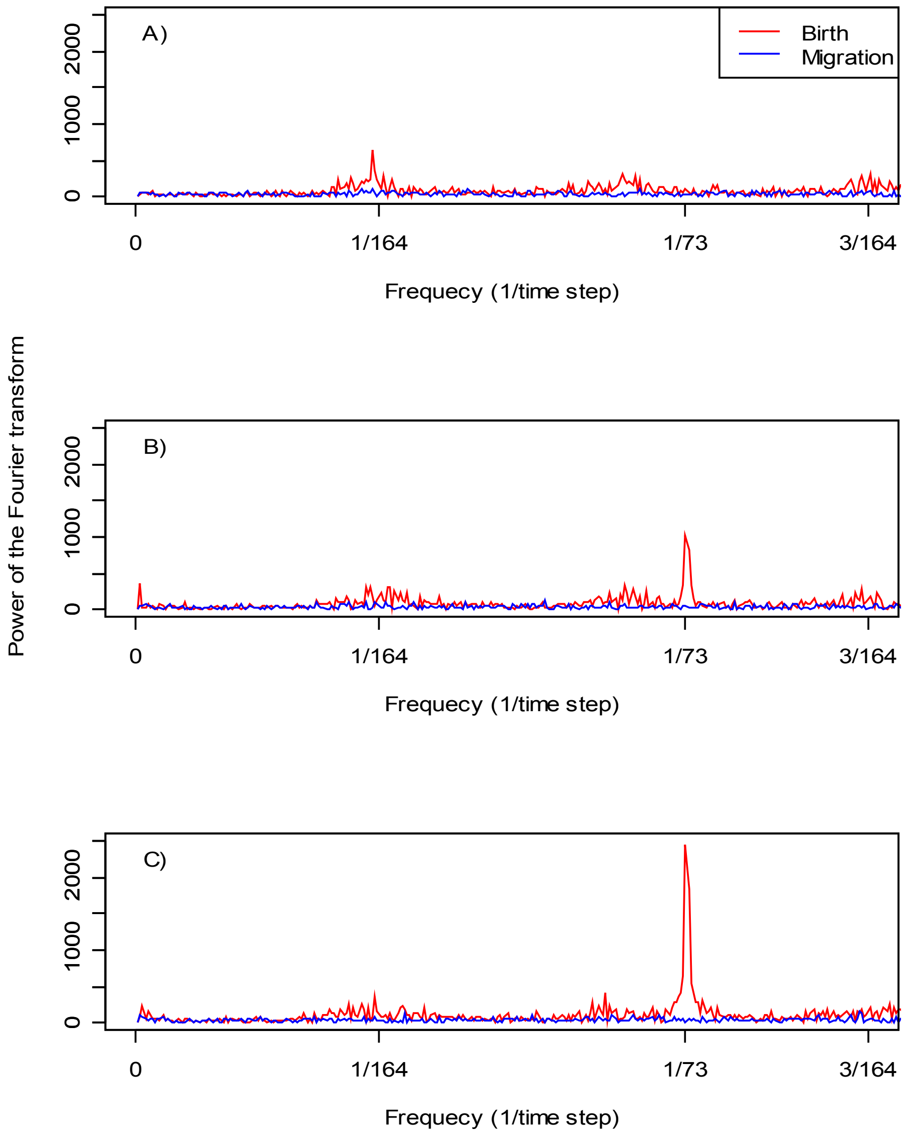


Figure 7: Spectra of birth (in red) and migration (in blue) for one replicate, at the population level, without seasonality (A), with an intermediate seasonal forcing (B) and a strong seasonal forcing (C). With increasing seasonality, we observe an increase of the peak at 1/73, because of the synchronization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

The introduction of seasonality in the model changes radically that pattern. Indeed the seasonality is a forcing at the population level. With increasing seasonal forcing, the different troops tend to synchronize together. When the seasonality is strong enough, all the troops are in phase, with their females cycling together (*cf.* 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, reproductive synchrony at the interbirth interval remaining comparable. For migration, seasonal forcing does not influence synchrony at the troop level. As a consequence, patterns at the population level are the same as the ones described earlier, without seasonality. Finally, no pattern is detected for infanticide.

IV- Discussion

Infanticide has significant effect on reproductive synchrony. More precisely, infanticide increases significantly the level of reproductive synchrony naturally present in a troop. In a non seasonal environment, this synchrony is mostly detected at the troop level, with the interbirth interval as a period. In each troop, migration follows reproduction and becomes synchronous at the interbirth interval as well, whereas infanticide never becomes synchronous. At the population level, a smaller level of synchrony is detected in reproduction at the interbirth interval, but no pattern is detected concerning migration or infanticide. Moreover, without seasonality, the different troops in the population remain mostly independent. When seasonality is added in the model, the annual period appears as a significant period of synchrony in birth, but is not present in migration. At the population level, seasonality synchronizes the troops together in phase. As a result, a very strong level of synchrony at the annual period is detected at the population level with a strong seasonal forcing. Migration remains unaffected by seasonality.

When infanticide is added to the control, reproductive synchrony increases significantly. In the model, when an infanticide occurs, females that have lost there infant resume cycling more quickly than at the end of the lactation period. More important, those females resume cycling at the same time, and tend then to cycle synchronously. Because of the stochastic processes in the model, if infanticide is too rare, females tend to desynchronise. When infanticide rate increases, more females are concerned by infanticide and put in phase at the same time when it occurs, and females are resynchronized more often. Those two processes explain the increase of reproductive synchrony with increasing infanticide. However, if infanticide is too frequent (with a higher rate than observed in reality and tested in the model), we can expect that females would start to be interrupted in their reproductive cycle too often to maintain a high level of synchrony. Indeed, at each event of infanticide, the females concerned would still resume cycling together, but they would not stay in phase long enough to see any particular period of synchrony emerging. We could then expect a decrease in synchrony at the interbirth interval with very high rate of infanticide. Finally, if infanticide is extremely high, we could expect that too many infant would be killed for the recruitment to the troop to be enough and the troop would not survive.

When infanticide is comparable to the reality, we observed that synchrony in migration increases as well. This can be explained by the fact that migration of males is directly linked the cycle of females in the troop concerned. Indeed, as explained earlier, the probability for a male to immigrate in a troop increases when there is more females in oestrus at the same time in that troop. As a consequence, when females are in phase with each others, more females happen to be cycling at the same time in a troop which makes it more attractive for males at this time. Contrarily, when the females are all pregnant or lactating, the attractiveness of the troop is very low, which causes emigration of males from the troop. Migration is then becoming synchronous in relation to rhythm of reproduction. However, we could expect that if all females in a troop are in phase, and so is migration of males, then males would enter the troop when all females are in oestrus, no infant would then be killed and infanticide would disappear. But migration is also dependent on the number of males present in the troop, which affect migration in the opposite way than number of cycling females. Indeed, if no females are cycling, males inside would tend to leave, and then the troop would become more attractive because of the low number of males present in it. The two opposite effects explain in part why the level of synchrony in migration is lower than in reproduction. Moreover, different random processes, in the number of cycles before conceiving for example, and other processes such as protection by the old dominant desynchronise females in a troop so that a situation where every females are strictly in phase never happens and infanticide never disappears.

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

When seasonality is added to the model, the annual period becomes significant in the reproductive synchrony. This was expected because seasonality affect directly the reproductive cycle of females through the probability of conception at the mating time. But migration does not follow reproduction, and does not seem to affected by the seasonality. Although it is a counter-intuitive result, it fits observations made on the field [Cheney2004]. A possible explanation could be that interbirth interval remains the most significant period in reproduction, even with a highly seasonal environment. Then migration would still synchronise in relation to reproduction, but only in relation to the most significant period. But this idea of explanation needs further analysis of the model to be tested and verified.

When synchrony is measured at the population level, despite the cases with seasonality, we generally measure a lower level of synchrony than at the troop level. This phenomenon is easy to understand, considering four cosine functions with the same period and random phases. Those four functions represent the time series of each troop. Summing those four function gives as a result a cosine function with the same period, and a phase and an amplitude depending on the phases of the four separate functions. Then, apart from the case when the phases of the four separate cosines are such as the amplitude of the sum is null, the sum always have a detectable period which would be the period of reproductive synchrony in our case. The significance of the synchrony being related to the amplitude of the signal, in the sum at the population level that amplitude depends on the phase of each troop. Hence, the significance of the synchrony at the population level does not give information on the level of synchrony at the troop level, but rather on lag in phase between the troops.

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-Condit1997],[Cheney2004],[Brockman2005]). Such a plot is really useful when the objective is to detect annual patterns in the distribution of births over time. However, as we have seen in the example of our model, the patterns of synchrony are not necessary with a period of one year. When seasonality is not considered, the main period of synchrony is the interbirth interval, which defers from one species to the other. In our case, the interbirth interval is 2.2 years. With this period as the only period in reproductive synchrony, nothing would be detected on a one year plot. Indeed, as the interbirth interval is not a multiple of one year, every year, the peak of births occurs later in the year. Over a long enough period of time, on a year basis, births are equally spread among the year. To detect patterns of synchrony with a different period than the year, it is then interesting to work on the whole time series rather than one year transformed data, using tools such as autocorrelogram or Fourier analysis to detect the significant periods. When seasonality is present, the seasonal forcing is explicitly on a one year or a multiple of one year basis. The one year plot is then interesting to see the emergence of patterns on an annual base.

Another interesting aspect of this study is how an individual behaviour can have a direct impact on the whole troop dynamic, and could even be detected by its influence on the whole population. Indeed, infanticide is primarily an individual behaviour, the male chooses alone to commit infanticide, based on the situation of the troop. But his decision directly influence the dynamic of the troop by affecting the reproductive cycle of the females in the troop, and then birth distribution, and recruitment to the troop, which could affect directly the survival of the troop. And affecting one troop, it can be at least measured at the population level. And even if it is not shown by our model, we can imagine that due to links between troops in a population that are not taken into account in the model, the influence of infanticide on one troop could be reflected on the other troops of the population.

Finally, the model developed in this study is interesting because of its generality. Indeed, although it has been explicitly used on baboons, the different parameters used in it are general enough to be fitted to any species where infanticide is present. The results discussed here could then be tested on other species with documented infanticide, such as other primates (hanuman langurs, red howlers, Thomas' langurs... [Schaik2000]), others mammals, especially carnivores such as lions [Packer1983] but also rodents, and even birds [Schaik2000]. That would allow to generate very general results on the behavioural ecology of infanticide and its impact on the individual and population dynamics.

References

[Alberts1995]: Susan C. Alberts and Jeanne Altmann; Balancing costs and opportunities: dispersal in male baboons. *The American Naturalist*,145:279-306, 1995

[Altmann2003]: Jeanne Altmann and Susan C. Alberts; Intraspecific variability in fertility and offspring survival in nonhuman primate: behavioral control of ecological and social sources, in *Offspring: Human Fertility Behavior in Biodemographic perspective*, 140-169. The National Academies Press, 2003

[Bentley-Condit1997]: Bentley-Condit, Vicki K. and Smith, E. O.; Female reproductive parameters of Tana River Yellow Baboons. *International Journal of Primatology*,18:581-596, 1997

[Brockman2005]: Brockman, Diane K. and van Schaik, Carel P.; Seasonality and reproductive function, in *Seasonality in Primates*, 269-305. Cambridge University Press, 2005

[Brockman2005a]: Brockman, Diane K. and van Schaik, Carel P., Seasonality in Primates, 2005

[Cheney2004]: Cheney, D. L. and Seyfarth, R. M. and Fisher, J. and Beehner, J. and Bergman, T. and Johnson, S. E. and Kitchen, D. M. and Palombit, R. A. and Rendall, D. and Silk J. B.; Factors affecting reproduction and mortality among baboons in the Okavango Delta, Botswana. *International Journal of Primatology*,25:401-428, 2004

[Clarke2008]: Clarke, P.M.R. and Henzi, Peter and Barett, Louise and Rendall, D.; On the road again: competitive effects and condition-dependent dispersal in male baboons. *Animal Behavior*,In press:in press, 2008

[Collins1984]: Collins, D. A. and Busse, C. D. and Godall, J.; Infanticide in two populations of savannah baboons, in *Infanticide: comparative and evolutionary perspectives*, 193-215. Aldine: New York, 1984

[Darling1938]: Frank Fraser Darling, Bird flocks and the breeding cycle, 1938

[Grimm1999]: Volker Grimm; Ten years of individual-based modelling in ecology: what have we learned and what could we learn in the future?. *Ecological Modelling*,115:129-148, 1999

[Henzi2003]: Peter Henzi and Louise Barett; Evolutionary ecology, sexual conflict, and behavioral differentiation among baboons populations. *Evolutionary Anthropology*,12:217-230, 2003

[Ims1990]: Rolf Anker Ims; On the adaptive value of reproductive synchrony as a predator-swamping strategy. *The American Naturalist*,136:485-498, 1990

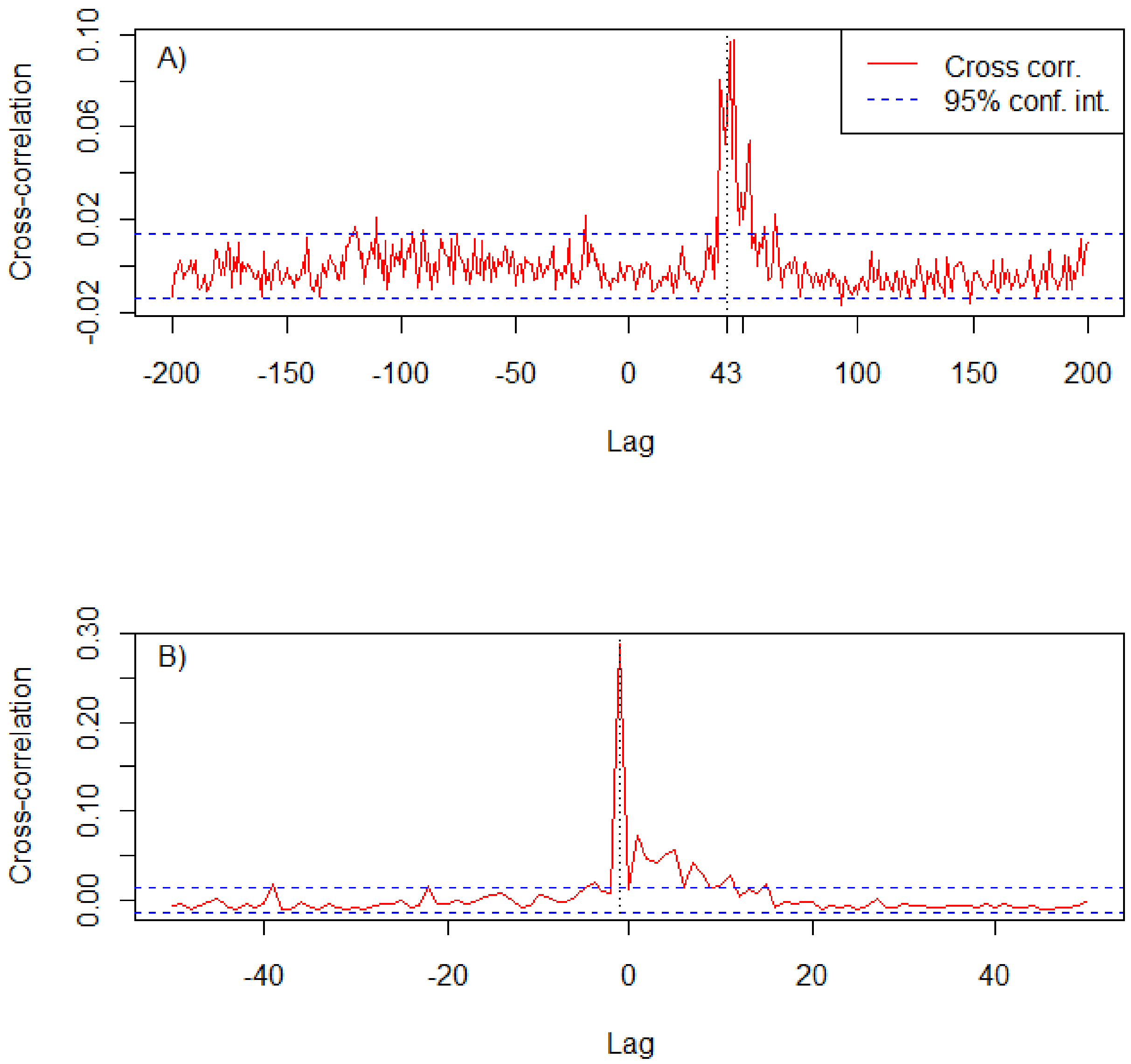
[Judson1994]: Judson, O. P.; The rise of the individual-based model in ecology. *Trends in Ecology & Evolution*,9:9-14, 1994

[Packer1983]: Craig Packer and Anne E. Pusey; Adaptation of female loions to infanticide by incoming males. *The American Naturalist*,121:716-728, 1983

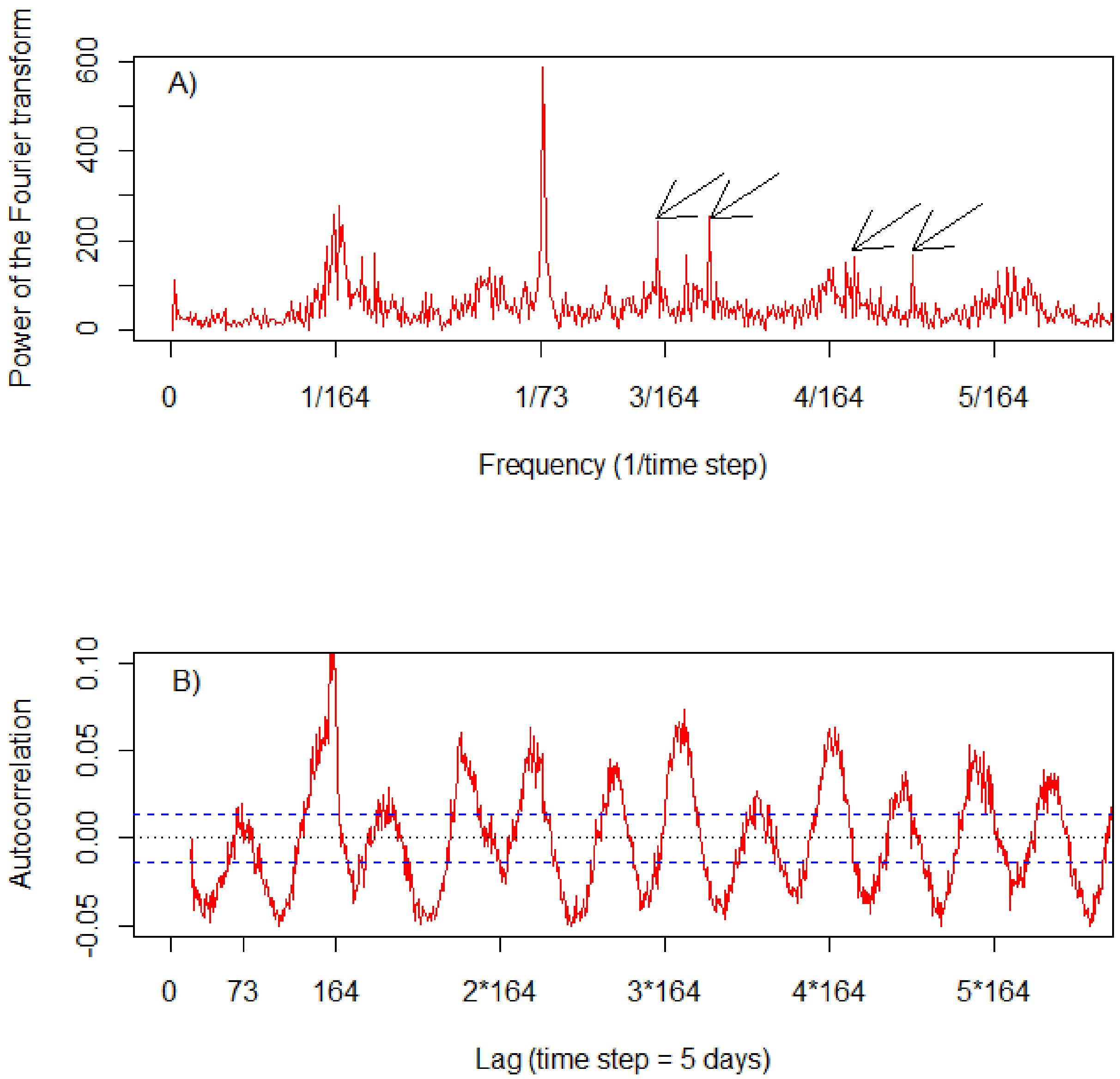
[Schaik2000]: van Schaik, Carel P. and Janson, Charles H., Infanticide By Males and its Implications, 2000

[Weingrill2000]: Weingrill, Tony; Infanticide and the value of Male-Female relationship in mountain Chacma Baboons. *Behaviour*,137:337-359, 2000

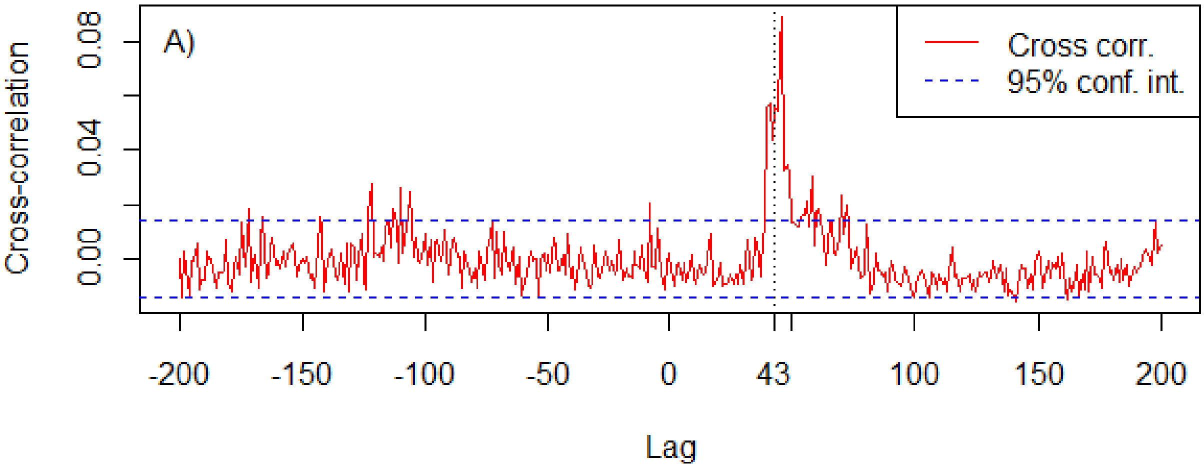
V- Annexes

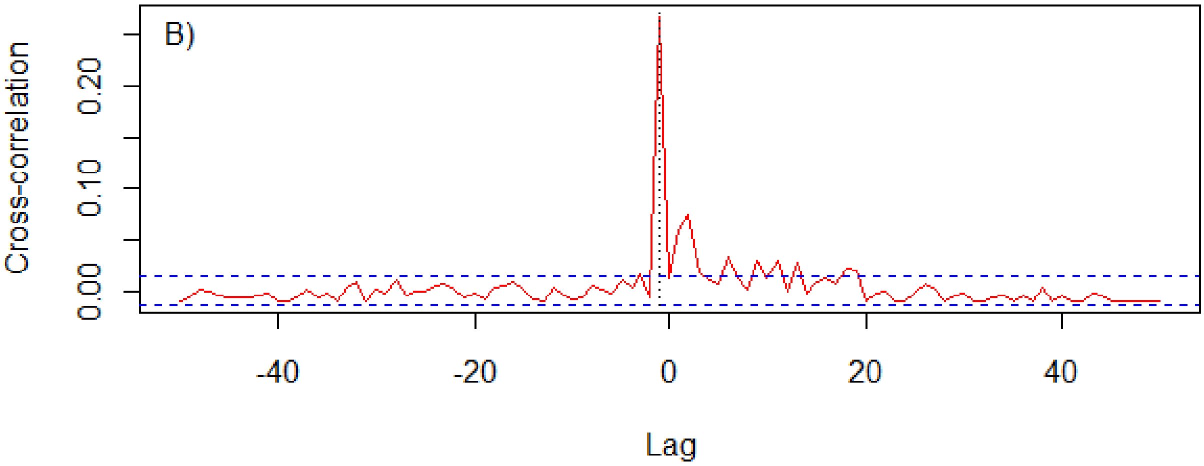


Annex 1: Cross correlation of infanticide versus birth (A) and infanticide versus immigration (B) at the group level in a non seasonal environment. The peaks on the cross correlograms show the presence of a particularly significant lag between two time series tested. Plot (A) shows that infanticides 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.

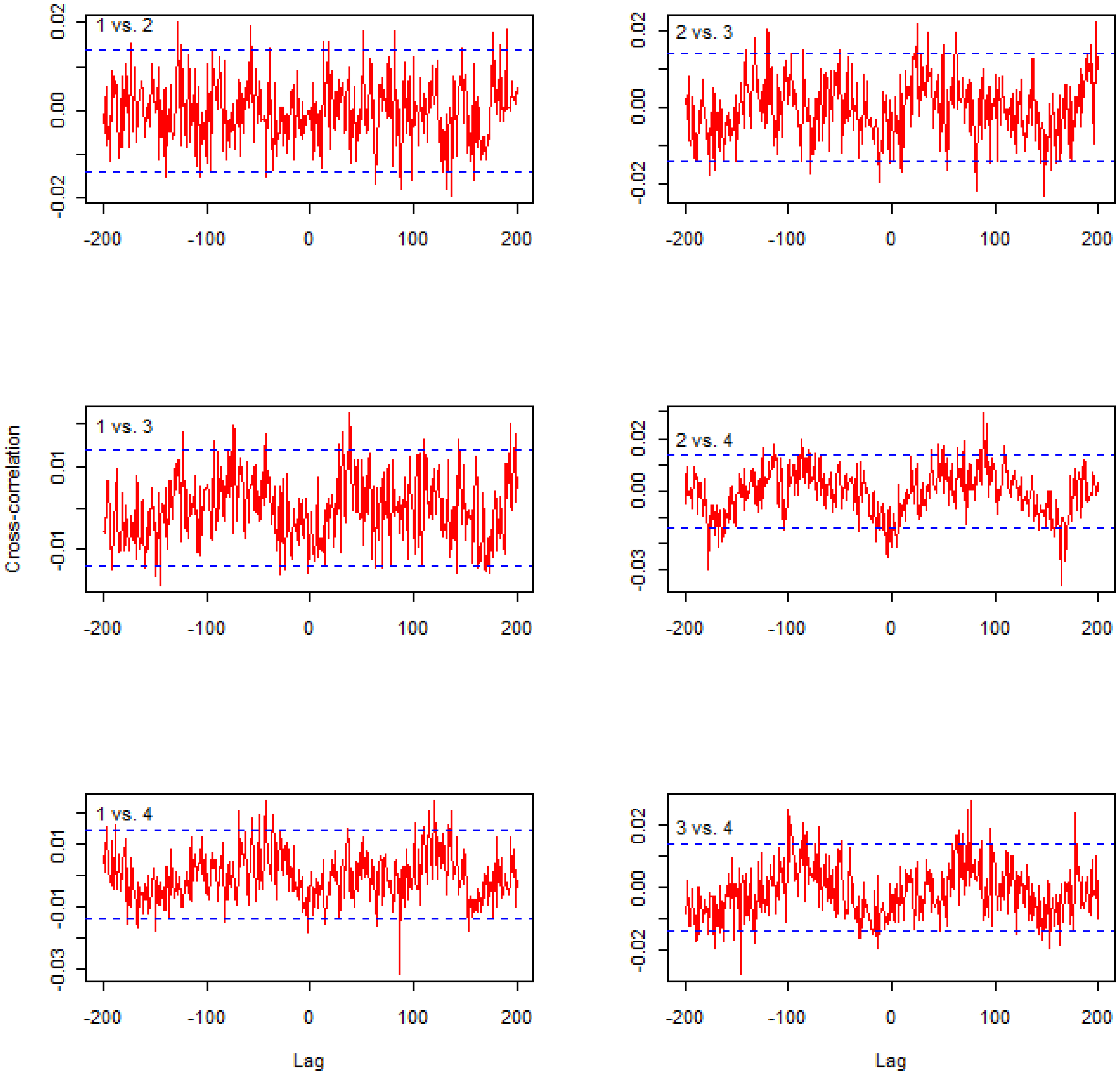


Annex 2: (A) Spectrum of births in a highly seasonal environment. This spectrum shows the presence of the two main frequencies, the interbirth interval (1/164) and the seasonality (1/73), but also new peaks that could possibly correspond to interference between those two main frequencies (arrows). (B) 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. 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 interval.

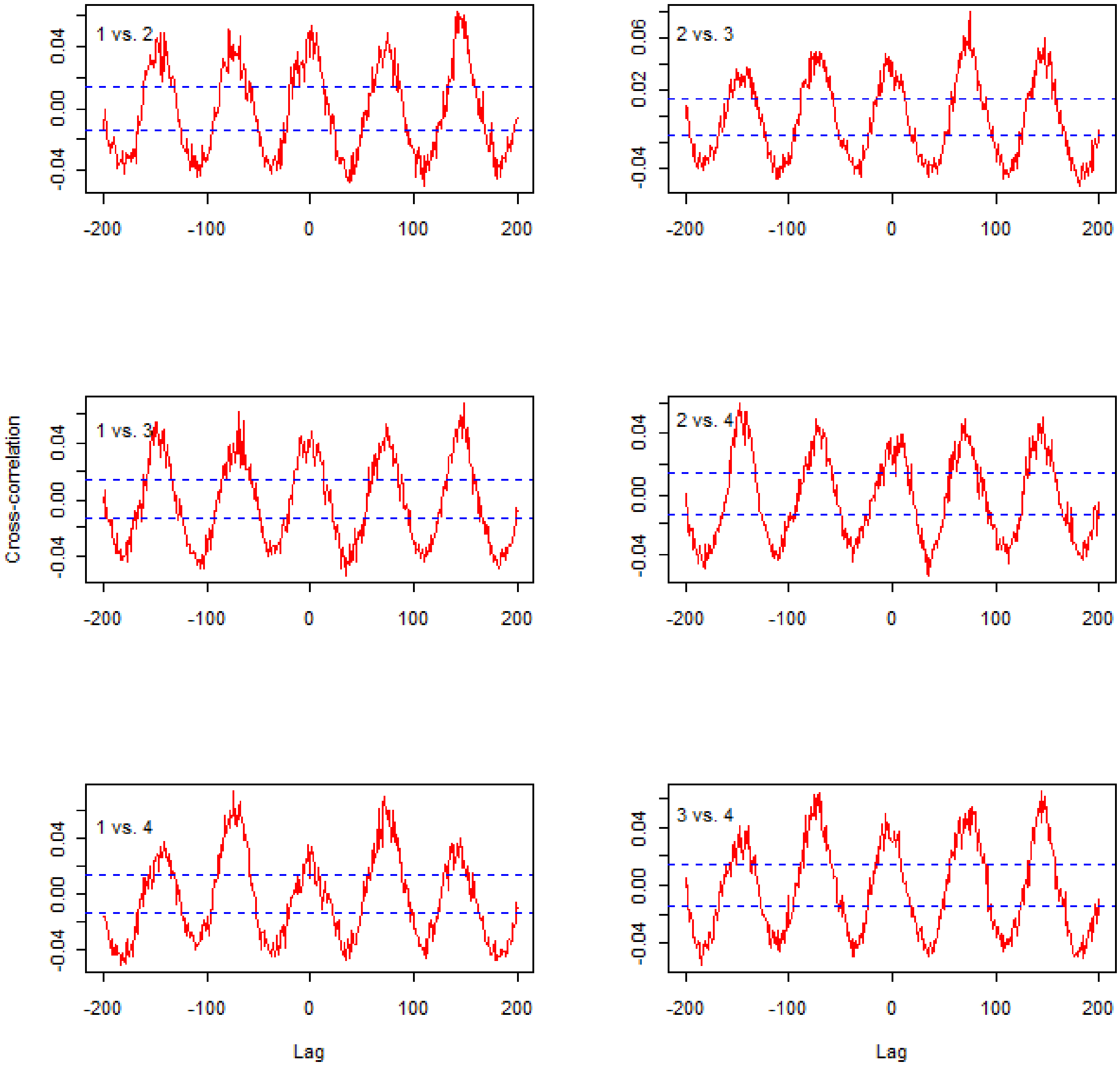




Annex 3: Cross correlation of infanticide versus birth (A) and infanticide versus immigration (B) at the group level in a seasonal environment. Plot (A) shows that infanticides are again generally followed by births 43 time steps later. Plot (B) shows that infanticide is again almost always preceded by an immigration. Seasonality does not affect cross correlation between infanticide, migration and birth. The blue lines represent the 95% confidence interval.



Annex 4: Cross correlation of birth between the different troops two by two in a non seasonal environment. Either no pattern or very small, non significant enough pattern are present between troops. When small patterns seem to appear, no reproducible results emerge. No really significant pattern of synchrony exist between the four troops of the population. The blue lines represent the 95% confidence interval.



Annex 5: Cross correlation of birth 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 emerge between the troops in a seasonal environment, all the troop being synchronized in phase. The blue lines represent the 95% confidence interval.

[Bentley-Condit1997][Cheney2004][Alberts1995][Henzi2003][Weingrill2000][Altmann2003][Clarke2008][Collins1984]