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## The spread of the 'Lapita people': a demographic simulation

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### Abstract

The authors used simulation to examine the viability of current theory concerning the expansion of the 'Lapita Cultural Complex' in the Southwestern Pacific region. Their simulation program, based on simple rules, generated a series of virtual colonies over time using a wide range of parameter values. These runs showed potential inconsistency about the speed of 'Lapita people', hence raising new questions about their social organization.

### Keywords:

Demographic simulation, Lapita diaspora, Southwestern Pacific region

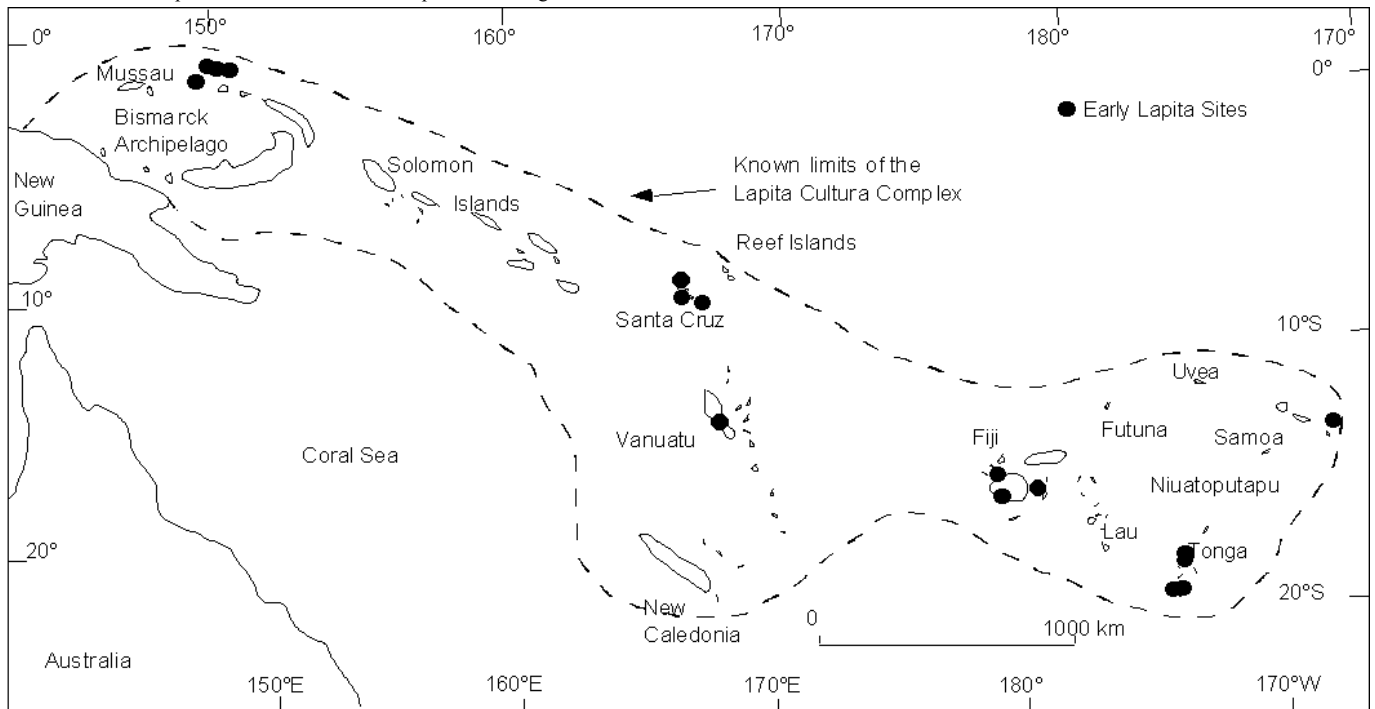
### Introduction

#### 1.1

In 1997, the archaeologist Patrick Kirch presented a model about the expansion of the 'Lapita people', who settled the archipelagos between New Guinea and Samoa, beginning 3,500 years ago (see [map 1](#)). These migrants were skilled navigators and are considered to be the ancestors of today's Pacific islanders. This extraordinary migration spanned 4,500 km over a very short period, only 300 to 500 years. It is the fastest known migration in prehistory. By simple arithmetic, Kirch estimated that the rate of expansion was 180 to 300 km per generation. To arrive at this figure, he used 20 years for a generation and divided the number of generations into 4,500 km. While the model is extremely elegant, it poses some problems when demographic values are added to build a virtual Lapita population.

#### 1.2

This paper, inspired by Kirch's model, presents a series of simulations investigating the demographics of this virtual Lapita population as it grows and migrates, producing new colonies through the western half of Oceania. The pattern of population distribution within these colonies will be discussed in relation to three demographic parameters (size of founding population, growth rate and migration rate). To put these virtual populations into an anthropological context, their distributions are compared to the distribution of Lapita archaeological sites.



Map 1: Distribution of the earliest Lapita sites in Oceania (after [Kirch, 1997:54](#))

### Kirch's model of the Lapita diaspora

#### 2.1

Let's review Kirch's model. He wrote ([1997:56, 62](#)):

As presently defined on the basis of archaeological surveys, the Lapita world began in the Bismarck Archipelago in the west, and extended through the island arcs of the Solomons and Vanuatu, down to New Caledonia in the south. It also reached across the 850 km wide ocean gap between the Santa Cruz Islands and Fiji, to encompass the Fiji, Lau, Tonga, and Samoa archipelagoes, as well as several smaller islands... A temporal cline extending from the Bismarck Archipelago south to New Caledonia and east to the Fiji-Tonga-Samoa region marks the path of the Lapita diaspora, a phase of population

expansion occurring in no less than three and no more than five centuries. The total straight-line geographic distance involved is about 4,500 km, so that the 'average' rate of dispersal or population movement was on the order of 9-15 km per year. Naturally, in an island world dispersal would not have taken place 1 km at a time, but rather in 'jumps' of varying distance. It may be more insightful, therefore, to think of this dispersal in terms of human generations. If each successive generation had a reproduction span of about 20 years, the Lapita diaspora required somewhere between 15 and 25 generations to accomplish. This suggests that, again on 'average', each successive generation moved eastwards or southwards somewhere between 180 and 300 km.

## Underlying assumptions for a demographic simulation of Lapita expansion

3.1

The model assumes that "...the expansion consisted of the creation of colonies that dispersed quickly, the daughter-colonies giving birth to other groups of colonies"<sup>[1]</sup> (Kirch, 1990:1229).

3.2

Spriggs (1997: 104-105) went further in his characterization of Lapita migrations. Using Anthony's (1990) general principles about the migration process, he qualifies Lapita migrations as: < type=>

- leap-frog: migration proceeds in jumps, large areas are by passed between settlements;
- resembling a stream: migration proceeds along a well defined route and often originates in highly restricted areas.
- self-propagating: migrants come from a population with a tradition of migrating, increasing the probability that migration will continue.

3.3

The simulation presented here utilizes these principles. Colonies are discrete populations with large distances between them. Migration proceeds eastward along the chain of archipelagoes. Migration is systematic and continues generation after generation. Therefore our founding population will be based in the Bismarck Archipelago<sup>[2]</sup> and will increase and expand eastward by sending out migrants to found new daughter colonies each generation (20 years) over a period of 300 to 500 years until it reaches Samoa.

## Rules used in the model

4.1

A founding population (colony 0) is initialized in the Bismarck Archipelago at time  $t=0$  years. This population increases at a certain rate (1% to 4% per year). At time  $t=20$  years (generation 1), a percentage of this population migrates (between 5 and 90%), founding daughter colony 1. These two populations continue to grow. At time  $t=40$  years (generation 2), colony 0 sends additional migrants to daughter colony 1 and daughter colony 1 sends migrants to found daughter colony 2. All populations continue to grow and send migrants at the same rates throughout each run. Therefore the model allows the formation of a maximum of 14 daughter colonies over 300 years or 24 daughter colonies over 500 years. (For the equations used in the simulation, see [appendix](#)). Note that the total number of colonies is equivalent to the number of daughter colonies + the founding population (colony 0).

## Values used for each parameter

5.1

The three parameters used in the model are the growth rate, the migration rate and the size of the founding population. Values for the first two are derived from historical sources and values for the founding population are assumed.

### Population growth rate

5.2

The upper limit for the growth rate in the past comes from the well known case of Pitcairn Island, settled by a mixed population of polynesians and europeans, which attained an annual growth rate of 3.7% from 1810 onward (Terrell, 1986:188-194). It is one of the highest ever recorded rate in a pre-modern society; a rate so high that Pitcairn islanders were doubling every 20 years. However, Lapita population growth rate probably never reached this high a growth rate. As noted by Sutton and Molloy (1989:32) "...It is unwise to assume that the Pitcairn case can be directly applied to precontact colonizations. First, the people on Pitcairn were almost exclusively drawn from cohorts with the highest age-specific fertility. Second, they were living in the absence of sociocultural constraints on sexual activity found in either society of origin. Finally they had a 18th century European technology, not a precontact Polynesian one, which is likely to have augmented survivorship."

5.3

Today, the population growth rate in specific countries in Oceania varies from 1.5 to 4% (see <http://www.census.gov>). Terrell (1986:194) notes that for the Pacific as a whole, growth rates have varied from 0.9% to 2.7% during the past 200 years. Therefore, to cover a wide range of possible growth rates in the simulation, we will use either 1%, 2%, 3%, 4%, 4% decreasing to 2% when the population reaches 8000 people, 4% decreasing to 0% when the population reaches 8000 people or 2% decreasing to 1% when the population reaches 5000 people. The rationale for using a variable growth rate is the idea that when islands are first settled, growth rates should be high and the growth rate should decrease when the population approaches carrying capacity.

### Migration rate

5.4

While population growth rates have been well studied, migration rates are harder to arrive at today and even more so 3,500 years ago. Ethnographic analogs<sup>[3]</sup> are rare and use modern means of transportation.

5.5

To estimate migration rates and to understand the effect that they would have on a population, lets look at the age structure of some typical oceanic populations whose growth rates are equivalent to those in our model (see [table 1](#)). In these populations, only half the people (58.5% on average) are adults (older than 15 years). About half of these would be men (29%), able to build and manage the 'migration canoes'. If we estimate that half the occupants of the canoes must be sailors (or adult men), then a 10% migration rate from the population as a whole would include 17% of all adult men in the original population<sup>[4]</sup>. A 20% migration rate would include 34% of adult men. Higher rates of migration would lead to very imbalanced sex ratios in the stay at home population. For the purpose of the model, we will use a 5, 10, or 20% migration rate per generation and investigate the consequences of values ranging over values less than the apparent upper limit of 20%.

**Table 1: Today's age structure and growth rate for several archipelagos in Oceania (Quid, 1998:896 and web site <http://www.census.gov>)**

Archipelago	Growth rate (%)	Children <15 years (%)	Adults 15 years (%)

Fiji	1.5	38	62
Marshalls	4.1	51	49
FSM	-	44	56
New Caledonia	1.9	31	69
French Polynesia	-	36	64
Solomons	3.7	47	53
Samoa	1.8	41	59
Vanuatu	2.8	44	56

### Founding population

#### 5.6

For the size of the founding population, we assumed values of 50, 100, 200 or 400 individuals. It is important to recognize that these numbers do not represent the entire population of the Bismarck Archipelago during the early Lapita period, only the portion that furnished successful migrants who managed to discover the next island eastward.

#### 5.7

In the model, we rejected the combination of parameters values that resulted in a total population at the end of the run greater than it is today in the Lapita area (about 1.5 million<sup>[5]</sup>) (Quid, 1998).

### Running the mode

#### 6.1

The model was built using STELLA software<sup>[6]</sup>. It was run to show the implications of the rules specified above -- the number of daughter colonies founded -- as well as to examine the relationships between the three demographic parameters. Although many runs were made using the range of values discussed, only the most representative are given here as graphs and tables. Graphs and tables give the population in each colony at the end of the run (t=300 years). From these population figures, we deduce the number of daughter colonies, defined as those with a minimum of 10 people, or about a canoe load.

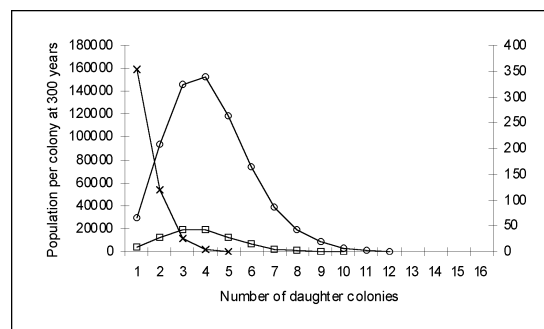
#### 6.2

Based on the rule for founding colonies (one per generation), one would expect the number of colonies to equal the number of generations. However, it does not. Using the widest range of parameter values, the number of daughter colonies was never greater than 11 over 15 generations (300 years) or 19 over 25 generations (500 years)<sup>[7]</sup>. This calls into question the speed estimated by Kirch. Indeed, if the values chosen for the parameters are realistic, then the rate of expansion must be much faster than the 180 to 300 km per generation estimated by Kirch. This model suggests a maximum speed of 237 to 409 km per generation. The disparity (between the number of colonies expected and the number of colonies obtained), which is an outcome of the parameter values chosen, is due to the restricted number of people available to found new daughter colonies. But which of these parameters is most critical in limiting the number of colonies founded?

#### 6.3

Using the widest range of values for the founding population (a factor of 8 between smallest and largest), for the growth rate (a factor of 4), and for the migration rate (a factor of 4), the number of daughter colonies was never less than 3 nor greater than 11 (a factor of 3.6) over 300 years (see Figure 1). Clearly the outcome is more sensitive to growth rate or migration rate than it is to the size of the initial population.

	Initial Population	Migration rate (%)	Growth rate (%)
-x-	50	5	1
-o-	200	20	4 to 2
--	5200	20	2

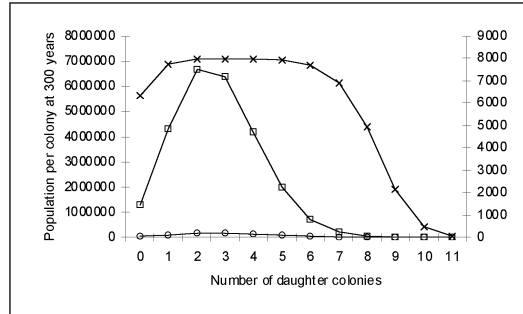


	Iteration 1 -x-	Iteration 2 -o-	Iteration 3 --
Colony 0	354	29,605	3,582
Daughter Colony 1	120	93,374	12,230
Daughter Colony 2	25	146,154	19,389
Daughter Colony 3	4	152,383	18,916
Daughter Colony 4	0	118,114	12,687
Daughter Colony 5	0	73,601	6,189
Daughter Colony 6	0	39,126	2,264
Daughter Colony 7	0	18,645	631
Daughter Colony 8	0	8,424	135
Daughter Colony 9	0	3018	22
Daughter Colony 10	0	559	3
Daughter Colony 11	0	58	0
Daughter Colony 12	0	4	0
Daughter Colony 13	0	0	0

**Figure 1:** Population distribution per colony at the end of the Lapita expansion (300 years). Using the widest range of parameter values, with colonies created every 20 years and with a cut-off of 10 people, the number of daughter colonies varies from 3 to 11 (in bold). On the graph, note that two different scales have been used. Iteration 1 has to be read with the right vertical axis. Iteration 2 and 3 have to be read with the left vertical axis.

6.4

It is intuitively clear that the ability to keep expanding eastwards is driven by the size of the population in the west. The higher the growth rate, the greater the population, the larger the number of migrants moving eastward and the more colonies that are founded. Using variable growth rates, the number of daughter colonies is driven by the initial growth rate and is equivalent to that obtained when using this initial growth rate throughout the run, although the total population may be quite different (see [Figure 2](#)). If growth rate seems to be relatively important, the acceptable range of values is narrow. It is indeed difficult to conceive of a total Lapita population that would be greater than is true today. The range for the migration rate appears to be more flexible.

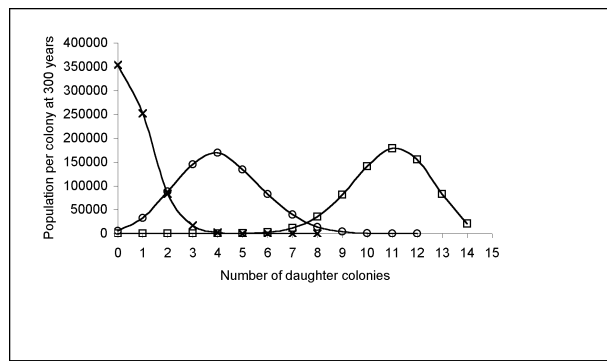


	-- Population per colony with a growth rate of 4%	-0- Population per colony with a growth rate of 4% to 2%	-x- Population per colony with a growth rate of 4% to 0%
Colony 0	1,295,612	29,605	6,328
Daughter Colony 1	4,318,707	93,374	7,738
Daughter Colony 2	6,683,714	146,154	7,956
Daughter Colony 3	6,365,442	152,383	7,985
Daughter Colony 4	4,167,849	118,114	7,973
Daughter Colony 5	1,984,690	73,601	7,911
Daughter Colony 6	708,818	39,126	7,682
Daughter Colony 7	192,876	18,645	6,918
Daughter Colony 8	40,182	8,424	4,949
Daughter Colony 9	6,378	3,018	2,138
Daughter Colony 10	759	559	463
Daughter Colony 11	66	58	53
Daughter Colony 12	4	4	4
Daughter Colony 13	0	0	0
Total population	25,765,097	683,065	68,095

**Figure 2:** Population distribution and number of daughter colonies founded at 300 years using an initial population of 200, a migration rate of 20% and variable growth rates. Daughter colonies are created every 20 years (one generation). Even though the number of daughter colonies are the same (11) for all runs, the total population is very different. On the graph, note that two different scales have been used. The 4% and the 4% to 2% growth rate curves have to be read with the left vertical axis. The 4% to 0% growth rate curve has to be read with the right vertical axis. On the table, note that the population in column 2 is far greater than today's population. This iteration has to be rejected.

6.5

A high number of daughter colonies can be an outcome of either high growth rates or high migration rates. The distribution of population within the daughter colonies would however be very different. A high growth rate leads to a very uneven population distribution, with almost everyone concentrated in the first few colonies. A high migration rate leads to a more even population distribution, with the peak shifted toward the east (see [Figure 3](#)). Because the Lapita diaspora is an exceptional event, there are no historic parallels from which to choose between these alternatives (high growth rate versus high migration rate). The best possible approach is to compare our virtual population distribution against the distribution of early Lapita sites.



**Figure 3:** Population distribution per colony at 300 years using an initial population of 100, a growth rate of 3% and variable migration rates. Daughter colonies are created every 20 years (one generation). At a migration rate of 5%, 95% of the population remains with the original colony. Therefore more people are concentrated in the west, near the Bismarck Archipelago. At a higher migration rate, the population concentration shifts eastward. A 30% migration rate or more, leads to a depopulation of the Bismarck Archipelago.

## Grounding the model in archaeology

### 7.1

Kirch (1997:263-276) noted 16 early Lapita sites (see table 2). These are located on 6 archipelagoes (Bismarck, Reef/Santa Cruz, Vanuatu, Fiji, Tonga, Samoa) (see map 1). None are listed for either the Solomon Islands or New Caledonia. This may represent sampling error, some areas have never been surveyed, others inadequately. It may also represent places that were skipped over during a leap-frog kind of migration.

**Table 2:** Inventory of the earliest Lapita archaeological sites (after Kirch, 1997:263-276)

Archipelago	Early Lapita Site
Bismarck/Mussau	Talepakemalai Etapakengaroasa Epakapaka Apalo
Reef/Santa Cruz	Nenumbo Nangu Malu & Bianga Mepala
Vanuatu	Malo
Fiji	Natunuku Yanuca Naigani
Tonga	Moala Pe'a Tongoleleka Faleloa
Samoa	To'aga

### 7.2

When we look at the distribution where there are sites, they appear relatively even from west to east. No region has a preponderance of early sites. If the pattern was driven by growth rate, we would expect to find a steep fall-off curve from west to east, with most sites concentrated in the Bismarck/Mussau. However, this does not appear to reflect the archaeological situation. The earliest Lapita sites distribution best fit a high migration rate type of curve, with a more even repartition. The question to be asked is: how high a migration rate would it take to account for such distribution? The answer seems to be above 20%. A 20% migration rate does not account for a high number of sites at the eastern end of the tail. From 50% up, the western colonies are depopulated at the end of the Lapita dispersal.

### 7.3

The 15 or 25 colonies implied by Kirch's model also require a very high migration rate. For example, to found 15 colonies over 300 years, with a founding population of 200 and a growth rate of 2%, necessitates a migration rate of 90%.

### 7.4

Such high rates imply sea-nomadism. A few such societies are known on the margins of Oceania: the Moken of Thailand and Burma and the Bajau of the Sulu Sea between Malaysia and the Philippines (Thorne and Raymond 1989:113-114). Interestingly enough, the Bajau speak austronesian languages as did the Lapita people (Pawley and Green, 1973). But virtually all other austronesian societies are sedentary.

## Conclusion

### 8.1

Simulations help to open doors or free the thinking process. It is not the norm to consider the Lapita peoples as sea gypsies. Archaeologists (like us) tend to see them as village agriculturists, a few of whom boarded canoes and migrated eastward. However, simulation does not necessarily help to choose among options. Both patterns of Lapita culture: sedentary or sea gypsy, are 'explainable' through demographic simulations. Moreover, these two options need not be exclusive. It might well be that during the earliest period of Lapita, people were sea gypsies, living on their canoes, practicing seasonal agriculture and long distance exchange. Later, they settled down, founding permanent villages, like the austronesians of today. Support for this hypothesis is the decrease in long distance exchange of obsidian, pottery and shell valuables from the early Lapita period to the late (Kirch, 1997:244).

## Notes

<sup>1</sup> "...d'une expansion fondée sur la création de colonies qui essaient rapidement, les colonies-filles donnant à leur tour naissance à d'autres groupes de colonies" (author's translation).

<sup>2</sup> The earliest and farthest west that archaeologists have so far been able to trace the Lapita trail is the Bismarck Archipelago.

<sup>3</sup> The best example known to the author is the British colonial scheme from the southern Gilberts to the Phoenix Islands (Kiribati) in 1937-1938, where a maximum of 15% of the population of one island (Beru) migrated. However, the average migration rate of the other 7 islands was about 3% (Maude, 1938:20; Maude 1968). Even 15% was only attained once and then only with coercion.

<sup>4</sup> Out of a population of 100, 29 are adult males (potential sailors). For a 10% migration rate, there are 10 migrants, 5 of who are sailors. This represents 17% of the adult men out of the original group (5 x 100/29).

<sup>5</sup> 1.5 million includes only native populations, excluding colonial immigrants.

<sup>6</sup> STELLA software is available from High Performance Systems, Inc, 45 Lyme Road, Hanover NH 03755, USA.

<sup>7</sup> The maximum number of daughter colonies is obtained with a growth rate of 4% decreasing to 2% or of 4% decreasing to 0% when the population reaches 8000 people and a migration rate of 20%.

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## Appendix

Equations used for the model (founding population of 200, migration rate of 10% per generation and growth rate of 2%).

Colony0(t) = Colony0(t - dt) + (Croiss\_Esp0 - Migra01) \* dt

INIT Colony0 = 200

INFLOWS: Croiss\_Esp0 = Colony0\*T<sub>x</sub>\_Croiss

OUTFLOWS: Migra01 = if time=20 then Colony0\*T<sub>x</sub>\_Migr else if time=40 then Colony0\*T<sub>x</sub>\_Migr else if time=60 then Colony0\*T<sub>x</sub>\_Migr else if time=80 then Colony0\*T<sub>x</sub>\_Migr else if time=100 then Colony0\*T<sub>x</sub>\_Migr else if time=120 then Colony0\*T<sub>x</sub>\_Migr else if time=140 then Colony0\*T<sub>x</sub>\_Migr else if time=160 then Colony0\*T<sub>x</sub>\_Migr else if time=180 then Colony0\*T<sub>x</sub>\_Migr else if time = 200 then Colony0\*T<sub>x</sub>\_Migr else if time =220 then Colony0\*T<sub>x</sub>\_Migr else if time=240 then Colony0\*T<sub>x</sub>\_Migr else if time= 260 then Colony0\*T<sub>x</sub>\_Migr else if time=280 then Colony0\*T<sub>x</sub>\_Migr else 0

Colony1(t) = Colony1(t - dt) + (Migra01 + Croiss\_Esp1 - Migra12) \* dt

INIT Colony1 = 0

INFLOWS: Migra01 = if time=20 then Colony0\*T<sub>x</sub>\_Migr else if time=40 then Colony0\*T<sub>x</sub>\_Migr else if time=60 then Colony0\*T<sub>x</sub>\_Migr else if time=80 then Colony0\*T<sub>x</sub>\_Migr else if time=100 then Colony0\*T<sub>x</sub>\_Migr else if time=120 then Colony0\*T<sub>x</sub>\_Migr else if time=140 then Colony0\*T<sub>x</sub>\_Migr else if time=160 then Colony0\*T<sub>x</sub>\_Migr else if time=180 then Colony0\*T<sub>x</sub>\_Migr else if time=200 then Colony0\*T<sub>x</sub>\_Migr else if time = 220 then Colony0\*T<sub>x</sub>\_Migr else if time =240 then Colony0\*T<sub>x</sub>\_Migr else if time=260 then Colony0\*T<sub>x</sub>\_Migr else if time=280 then Colony0\*T<sub>x</sub>\_Migr else 0

Croiss\_Esp1 = Colony1\*T<sub>x</sub>\_Croiss

OUTFLOWS: Migra12 = if time=40 then Colony1\*T<sub>x</sub>\_Migr else if time=60 then Colony1 \*T<sub>x</sub>\_Migr else if time = 80 then Colony1\*T<sub>x</sub>\_Migr else if time=100 then Colony1\*T<sub>x</sub>\_Migr else if time=120 then Colony1\*T<sub>x</sub>\_Migr else if time=140 then Colony1\*T<sub>x</sub>\_Migr else if time=160 then Colony1\*T<sub>x</sub>\_Migr else if time=180 then Colony1\*T<sub>x</sub>\_Migr else if time=200 then Colony1\*T<sub>x</sub>\_Migr else if time=220 then Colony1\*T<sub>x</sub>\_Migr else if time=240 then Colony1\*T<sub>x</sub>\_Migr else if time=260 then Colony1\*T<sub>x</sub>\_Migr else if time=280 then Colony1\*T<sub>x</sub>\_Migr else 0

Colony10(t) = Colony10(t - dt) + (Migr910 + Croiss\_esp10 - Migr1011) \* dt

INIT Colony10 = 0

INFLOWS: Migr910 = if time = 200 then Colony9\*T<sub>x</sub>\_Migr else if time = 220 then Colony9\*T<sub>x</sub>\_Migr else if time = 240 then Colony9\*T<sub>x</sub>\_Migr else if time = 260 then Colony9\*T<sub>x</sub>\_Migr else if time = 280 then Colony9\*T<sub>x</sub>\_Migr else 0

Croiss\_esp10 = Colony10\*T<sub>x</sub>\_Croiss

OUTFLOWS: Migr1011 = if time = 220 then Colony10\*T<sub>x</sub>\_Migr else if time = 240 then Colony10\*T<sub>x</sub>\_Migr else if time = 260 then Colony10\*T<sub>x</sub>\_Migr else if time = 280 then Colony10\*T<sub>x</sub>\_Migr else 0

Colony11(t) = Colony11(t - dt) + (Migr1011 + Croissesp11 - Migr1112) \* dt

INIT Colony11 = 0

INFLOWS: Migr1011 = if time = 220 then Colony10\*T<sub>x</sub>\_Migr else if time = 240 then Colony10\*T<sub>x</sub>\_Migr else if time = 260 then Colony10\*T<sub>x</sub>\_Migr else if time = 280 then Colony10\*T<sub>x</sub>\_Migr else 0

Croissesp11 = Colony11\*T<sub>x</sub>\_Croiss

OUTFLOWS: Migr1112 = if time=240 then Colony11\*T<sub>x</sub>\_Migr else if time=260 then Tx\_Migr\*Colony11 else if time=280 then Colony11\*T<sub>x</sub>\_Migr else 0

Colony12(t) = Colony12(t - dt) + (Migr1112 + Croissesp12 - Migr1213) \* dt

INIT Colony12 = 0

INFLOWS: Migr1112 = if time=240 then Colony11\*T<sub>x</sub>\_Migr else if time=260 then Tx\_Migr\*Colony11 else if time=280 then Colony11\*T<sub>x</sub>\_Migr else 0

Croissesp12 = Colony12\*T<sub>x</sub>\_Croiss

OUTFLOWS: Migr1213 = if time=260 then Colony12\*T<sub>x</sub>\_Migr else if time=280 then Colony12\*T<sub>x</sub>\_Migr else 0

Colony13(t) = Colony13(t - dt) + (Migr1213 + Croissesp13 - Migr1314) \* dt

INIT Colony13 = 0



Croiss\_esp8 = Colony8\*Tx\_Croiss

OUTFLOWS: Migr89 = if time = 180 then Colony8\*Tx\_Migr else if time = 200 then Colony8\*Tx\_Migr else if time = 220 then Colony8\*Tx\_Migr else if time = 240 then Colony8\*Tx\_Migr else if time = 260 then Colony8\*Tx\_Migr else if time = 280 then Colony8\*Tx\_Migr else 0

Colony9(t) = Colony9(t - dt) + (Migr89 + Croiss\_esp9 - Migr910) \* dt

INIT Colony9 = 0

INFLOWS: Migr89 = if time = 180 then Colony8\*Tx\_Migr else if time = 200 then Colony8\*Tx\_Migr else if time = 220 then Colony8\*Tx\_Migr else if time = 240 then Colony8\*Tx\_Migr else if time = 260 then Colony8\*Tx\_Migr else if time = 280 then Colony8\*Tx\_Migr else 0

Croiss\_esp9 = Colony9\*Tx\_Croiss

OUTFLOWS: Migr910 = if time = 200 then Colony9\*Tx\_Migr else if time = 220 then Colony9\*Tx\_Migr else

if time = 240 then Colony9\*Tx\_Migr else if time = 260 then Colony9\*Tx\_Migr else if time = 280 then Colony9\*Tx\_Migr else 0

ColonyTot = Colony1 + Colony2 + Colony3 + Colony4 + Colony5 + Colony6 + Colony7 + Colony8 + Colony9 + Colony10 + Colony11 + Colony12 + Colony13 + Colony14

Tx\_Croiss = 0.02

Tx\_Migr = 0.1

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