COMPUTER SIMULATION OF HOST AND SEVERAL PARASITE SPECIES WITH AGEING

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ABSTRACT. – The possible coexistence of one host, one aggressive parasite and one non-lethal parasite is simulated using the Penna model of biological ageing. If the aggressive parasites survive the difficult initial times where they have to adjust genetically to the proper host age, all three species may survive, though the host number may be diminished by increasing parasite aggressivity. Simulations of more diversified conditions considering more than two parasite species underline the importance of synchronization for long term survival.

The extinction of biological population is an extreme event (Albeverio et al. 2006) and in an ageing simulation like the Penna model can be due to random fluctuations for small populations (Pal 1996) or due to unfavourable conditions for large populations (Malarz 2007). We had earlier applied these computer simulation methods to one host species and one parasite species, where the parasite needs to attack the host at one specific age of the host (Stauffer et al. 2007). Now we generalise this simulation to two parasite species, and assume that one of them also kills the host with some probability and the other (non-lethal) parasite with some other probability (Lampe 1984).

All these simulations were based on the at present most commonly used computer model of biological ageing, the Penna model (Penna 1995, Stauffer et al. 2006) of Medawar’s mutation accumulation; see e.g. Mueller & Rose (1996) and Charlesworth (2001) for alternative implementations of mutation accumulation. The genome is represented by 32 bits, where a zero bit means healthy and 1 means sick. The position of a 1-bit in this bit-string gives the age interval from which on a life-threatening disease affects the health. If three such diseases are active (3 bits set to 1 up to that age), the individual dies at the age corresponding to the position of the third 1-bit. In addition, all individuals die independently of their age with the Verhulst probability N(t)/K at time step t, where N is the current population size and K is often called the carrying capacity. At each iteration, each living mature individual of age 8 and above gives birth to $B$ offspring, with $B = 3$ for the host and $B = 14$ for the parasite. At each birth, one random mutation is made for all offspring by flipping a randomly selected bit from 0 (healthy) to 1 (sick). (If it is 1 already it stays at 1: no new mutation). Typically, $10^4$ iterations were averaged over after the populations had reached roughly a dynamic equilibrium of births and deaths. More details on the Penna model of 1995 are given in many articles and books (Stauffer et al. 2006, Stauffer 2007) and in our appendix. [For example, this Penna model predicted (Altevolmer 1999) some counter-intuitive (Mitteldorf & Pepper 2007) effects of predators on ageing (Reznick et al 2004)].

Many other mathematical or computational studies of host-parasite systems and their (co-) evolution were published (see e.g. van Baalen & Sabelis 1995, Martins 2000, Restif & Koella 2003, Tseng 2006) but most do not include the individual ages, while our aim is the emergence of age synchronisations. Only Martins 2000 included ageing, using the same Penna model as we do but applying it to a comparison of sexual versus asexual host reproduction in the presence of parasites.

With this standard model, hosts and parasites are simulated together, using separate Verhulst factors with the carrying capacity of the parasites ten times bigger than that of the host. In contrast to the hosts, the parasites at each iteration make 100 attempts to invade a living host of their desired age. (These desired host ages are at the beginning distributed randomly between zero and 31). If all 100 attempts were unsuccessful, they die. Otherwise they have enough food provided the host age is at least 10 for the first (aggressive) species of parasite called P1, and is at least 8 for the second non-lethal species of parasite called P2. If the host is too young, then again the parasite dies; if not it survives and ages.

We also mutated, randomly and continuously, the desired host age stored in the genome of each parasite. Then at birth of a parasite, not only the usual bit-string genome is mutated but also its desired host age. With 25 percent probability it increases by one unit, with 25 percent probability it decreases by one unit, and in the remaining 50 percent of the cases it stays constant. Initially we have equally strong populations of host and each parasite species.

Let $i = 1, 2, 3$ denote the aggressive parasites, the non-lethal parasites, and the hosts, $K_i$ with $K_i = 10K$, the carrying capacities, and $K_i$ is ten times the initial popula-
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Fig. 1. - Time dependence of host number, for fixed aggressiveness $b$ of parasite P1 against the other parasite P2, and for varying aggressiveness $a$ of P1 against the host.

Fig. 2. - As previous figure but for the number of aggressive parasites P1.

Fig. 3. - Final distribution of genetically programmed desired host ages for the two parasite species P1 (right) and P2 (left). The initial distribution is flat, between ages 1 and 31.

Fig. 4. - Ten times bigger initial populations (of all three species) than in Fig. 2 avoids the parasite P1 extinction seen in some cases of Fig. 2 at short times. The line for $a = 0.5$ shows the enormous later fluctuations in the host numbers.

Fig. 5. - Example with one lethal and two nonlethal parasite species; P1 can kill both non-lethal species with the same probability $b$. For $a = 0$ the results look similar.

with $b = 0.1$ and various aggressivities $a$ in our simulations. Thus only the aggressive parasite has the usual Verhulst factor for $N_j$, while both the host number $N_i$ and the number $N_2$ of non-lethal parasites are negatively influenced by the $N_i$ aggressive parasites.

Fig. 1 shows the time dependence of the host population and Fig. 2 that of P1. The one for P2 is not shown since it barely changes when we change parameters and always survived. Fig. 3 shows that the distributions of the desired host ages have self-organized to rather sharp peaks centred about the given minimum host ages of 10 for P1 and 8 for P2.

Small populations subject to random fluctuations always die out if observed long enough (Pal 1996). “Small” means here that the fluctuations in the population size are much smaller than the average population size. This effect is responsible for the extinction of P1 seen in some of the curves of Fig. 2. With a ten times bigger population, the time consuming simulations of Fig. 4 show survival of P1 where before we had extinction: Instead of extinction we now see a minimum. These surviving para-
sites P1 later reduce the host population.

We also simulated three instead of two parasite species, adding a non-lethal P3 feeding on host of age 6 and above, compared with 10 and 8 for P1 and P2. Fig. 5 shows an example of coexistence; in another sample differing only in the random numbers the parasite P1 became extinct. The analog of Fig. 3 now gives three peaks (not shown).

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More complex is a system of three aggressive parasites $P_1, P_2, P_3$ plus one host: each parasite species $i$ kills the host with probability $\sim aN_i$, while parasites kill each other with probability $\sim bN_i$ in a hierarchical way: $P_3$ kills $P_1$ and $P_2$, $P_2$ kills $P_1$. Usually one of the species dies out but Fig. 6 shows an example of coexistence for small $b = 0.001$, $a = 0.01$ and again minimum food ages 10, 8 and 6 for $P_1$, $P_2$ and $P_3$, respectively. The three self-organised distributions of desired food ages show again nicely the importance of synchronisation.

Finally we simulate one aggressive and four non-lethal parasite species, with needed host ages of 10, 8, 6, 4 and 2, respectively, in Fig. 7. Fig. 8 corresponds to reality, as observed near Kiel in northern Germany among 200 to 450 hosts of *Mikiola fagi* (Hartig, 1839) (European beech tree gall midge), and five parasite species attacking at different times of the year. This synchronisation of lives is what we simulated here.

In summary, for three to six species as well as in the previous study (Stauffer et al. 2007) of only one type of parasites, the proper distribution of desired host ages emerges in the parasite genomes, provided the aggressive parasites do not go extinct during this process of self-organisation.

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