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Characterizing the Phase Transitions between Stable Equilibrium and Periodic Oscillations in Predator-prey Population Dynamics: A Theoretical Appraisal from an Extended Nicholson & Bailey Model

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Author's contribution

The sole author designed, analysed, interpreted and prepared the manuscript.

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ABSTRACT

Multi-phase patterns with more or less sharp phase transitions, first highlighted in thermodynamics, have progressively revealed having wider relevance, being encountered in various other contexts, for example fluid mechanics, and can even occur in the interactive dynamics in biological populations involving two or more species that share opposite interests, such as predator-prey or parasite-host pairs of species. In the latter, the pattern of abundances of both interacting species usually reaches an equilibrium level which can be either *stable* or *cyclic* (with large *periodic oscillations* in the latter case). Both alternative modes are separated by well-define boundaries and, accordingly, can relevantly be described in terms of phases and phase transitions. While this has recently been approached from very general perspectives, a more focused analysis is still lacking, regarding the nature of the phase transitions between stable and oscillatory equilibria and – still more importantly – how the nature of these phase transitions may possibly depend (or not) on the biological and contextual factors driving the parasite-host interactive dynamics. These issues are

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addressed hereafter, on a theoretical basis, yet intimately related to the real field context, by taking advantage of a newly derived extension of the classical Nicholson & Bailey model of parasite-host interactions. Highlighted in particular are the possibility of either first-order, second-order or continuous phase-transitions, depending on (i) the respective own dynamics of both host and parasite, (ii) the density of feeding resource for the host, (iii) the level of migration exchange in a meta-population context.

Keywords: Host-parasite; relaxation oscillations; first order transition.

1. INTRODUCTION

Predator-prey relationship *sensu lato* is one of the most ubiquitous form of interactions between individuals within animal communities and, as such, has caused much practical concern and also prompted strong speculative interest since a long time [1-4]. Predator-prey interactive relationships can take several, various aspects, among which the more commonly encountered is probably the parasite (especially parasitoid) *versus* host interactions, especially frequent in insects – the richest and most diversified animal group worldwide [5-7].

One major and admittedly remarkable aspect of predator-prey interactions is the crudely contrasted alternative forms that the outcome of these interactions can take. These alternative forms being either [5,7]:

I. a *stable equilibrium* between the respective abundances of the predator and the prey, with the equilibrium level depending, of course, on the relative performances (reproduction rate, detection /escape abilities …) of each of the two partners involved, or
II. a more or less strong, *oscillating* pattern between the relative abundances of the predator and the prey, with usually regular cycles showing *periodic* oscillations: Fig. 1.

These two contrasted patterns of interactions are all the more remarkable that both patterns can be alternatively encountered within one and the same predator-prey system, involving the same couple of interacting species (see Figs. 1 & 2, with S_1 and S_2 as the two phases where the densities of the host and the parasite both reach *stable* respective equilibrium, while Os is the phase of *oscillatory* equilibrium for both the host and the parasite densities).

This somewhat surprising situation has contributed, in turn, to draw specific attention – and indeed to seriously puzzle – not only the naturalists themselves but also, and perhaps still more, those people having practical concern, or economical interest, in the exploitation of various kind of natural resource impacted by this common phenomenon [3-9].

Hence the incentive to better understand the ins and outs of the mechanism involved in such predator-prey interactions on a theoretical basis.

While this improved understanding has much to do – as a whole – with biological and ecological analysis, one particular aspect (of admittedly rather speculative interest) has more in-depth formal connections with Physical Sciences.

Moreover, these two sharply contrasted patterns, separated from each-other by acute reciprocal delimitations (mutual boundaries) are, as such, evocative of a multi-phase (here two-phase) kind of structuring. In this respect, two questions deserve being more specifically addressed.

The first question, of more speculative interest, is: which kind(s) of phase transitions (referring to the usual classification by EHRENFEST [10]) is (are) expected to delimit the “stable equilibrium” phases from the “periodic-oscillation” phase in the interacting system predator-prey; that is, are these phase transitions first-order, second-order, or simply exhibiting smooth transition?

The second, more pragmatic question is: what kind of influence – if any – can the “periodic-oscillation phase” have on the drasticity of the predator-prey interaction: An exacerbating influence or, conversely a relaxing role, or still no influence at all?

Such questions preferably call for a theoretical approach, based on the available models of predator-prey interactions, taking advantage of the fact that interactions of this kind straightforwardly lend themselves to mathematical treatment. Indeed, theoretical models dedicated to predator-prey interactions have been largely developed; the still more frequently referenced being the classical “Nicholson and Bailey model”, especially focused on parasite-host interactions [5,8]. Yet, the original version of this model still calls for some improvements in order to more closely – while still approximately – fit the realistic field conditions. Among required improvements are:

I. Taking in account of the *unavoidably limited* available feeding resource for the host (a limitation which combines with the level of parasitism pressure to govern and regulate the abundance of the host);
II. Accounting also for the so-called “meta-population” context, that is to say, integrating the contribution of some immigration / emigration of both predator and prey individuals circulating between more or less closely neighboring populations.

To my knowledge, no currently available model relevantly answers all these desired improvements, so that I have developed, at first, an *extended* theoretical model, designed to cope with these two additional requirements. In a second stage, this newly designed model is implemented to succinctly address and tentatively answer the two main questions featured above, which form the main objective of this work.

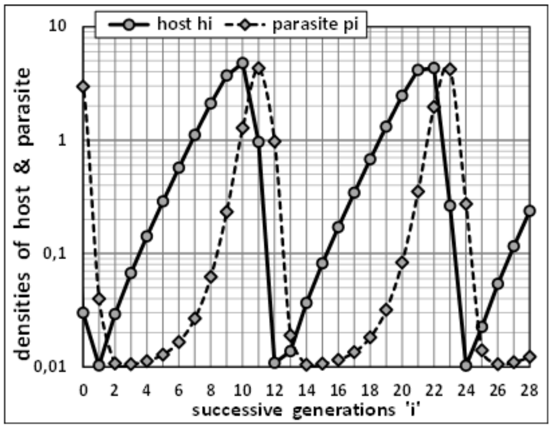

Fig. 1. An example of oscillatory equilibrium in host-parasite dynamics. *Discs*: density of the host species; *diamonds*: density of the parasite species; [computed from equations (11) & (12) with K = 100, r = 2.0, a = 6.0, f = 0.3, v = 1, $e_H = e_P = 0.01$]

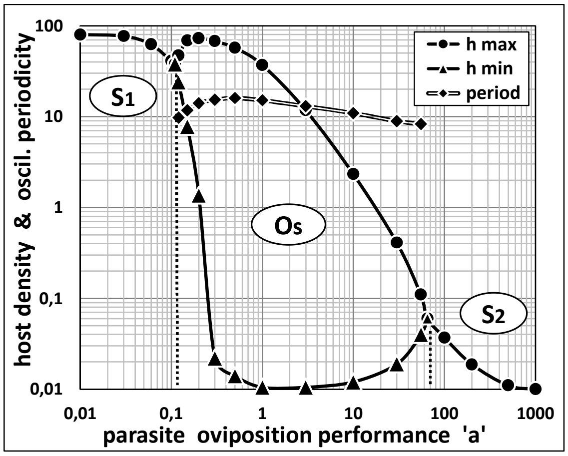

Fig. 2. Host density plotted against increasing reproductive (oviposition) performance ‘a’ of the parasite. *Discs*: density of the host in the stable equilibrium phases (S_1, S_2) and upper (peak) density of the host in the oscillatory phase (O_s); *triangles*: lower (trough) density of the host in the oscillatory phase; *diamonds*: periodicity of the oscillation cycle in term of number of generations. [computed from eq. (11) with K = 100, r = 2.0, f = 0.3, v = 1, $e_H = e_P = 0.01$]

2. THE PROPOSED EXTENSION OF THE NICHOLSON & BAILEY MODEL

The newly designed predator-prey model – more specifically focused on parasite-host interactions – is described in more details in the Appendix. In terms of host-parasite relationships, the relevant time unit to be considered is the generation duration (usually common to both the parasite and the host). Dedicated models are thus expressed in discrete-time with the time increment ‘i' labelling the successive generations of the host and parasite.

Let then ‘$\mathbf{h}_i$’ and ‘$\mathbf{p}_i$’ be the densities (numbers of individuals per unit area of field investigation) of the host and of the parasite respectively, at the common generation labelled ‘i'. Consider now the respective *own* dynamics of the parasite and of the host species (with the “own” dynamics of the host being understood in the absence of the parasite). These own dynamics are characterized quantitatively by the parameters given below.

*For the *parasite* (predator) species: ‘**v**’, ‘**f**’ and ‘**a**’, with ‘**v**’ as the average number of viable parasite individuals issued from each parasitized host-individual, ‘**f**’ as the proportion of mated (and thus egg-laying) females within the whole population of parasites and ‘**a**’ as the mean foraging area of an ovipositing parasite-female. In the following, this last parameter, **a**, is considered as the main distinctive parameter, singularizing and thus differentiating the reproductive own performance of a parasite species.

*For the *host* (prey) species: ‘**r**’ and ‘**K**’, with ‘**r**’ as the inherent rate of increase of the host individual (that is, in absence of any limitation in resource availability for the development of host individuals). Now, as in fact, the available feeding resource for the host is always more or less limited in nature, it is necessary to consider also a parameter accounting for this limitation: ‘**K**’, the so-called “resource carrying capacity” for the host population. More precisely, K is the density of host individuals that could ultimately be fed by the hypothetically exhaustive consummation of the available resource.

In addition, let ‘$\mathbf{e}_H$’ and ‘$\mathbf{e}_P$’ be the additional contributions of immigration, more exactly the balance between immigration and emigration of host individuals (resp. of parasite individuals), in complement to the host and parasite densities, generated *in situ*, within the studied population system itself.

3. STABLE EQUILIBRIUM AND OSCILLATORY EQUILIBRIUM: TWO CHARACTERISTIC PHASES IN HOST-PARASITE DYNAMICS

It has long been recorded that in predator-prey dynamics in general, and in host-parasite dynamics in particular, the relative abundances (densities) of each the two interacting species progressively reach equilibrium values respectively. These equilibrium values, however, may be either *stable* or, on the contrary, more or less strongly *oscillatory*, with a characteristic pattern, as exemplified in Fig. 1. The oscillatory pattern, when it occurs, is characterized by a constant period as well as constant shape of oscillations with a very sharp decreasing rate and a comparatively slower increasing rate, especially as regards the host-oscillations (Fig. 1). In addition, the oscillations of the host and of the parasite densities have (of course) the *same* periodicity, with the parasite oscillations being yet slightly out of phase (slightly delayed) as compared to the host oscillations (Fig. 1).

With increasing reproductive performance of the parasite (here, improved oviposition efficiency ‘a’ of the mated female of parasite species) the respective densities of the parasite and the host pass successively across three phases of equilibrium, labelled respectively S_1, Os, S_2 (see Figs. 2 and 3 for a typical example):

I. a phase “S_1” of *stable* equilibria, where the host density is at a high level, yet monotonically decreasing with increasing parasite reproductive performance ‘a’, while the parasite density increases monotonically – and rather drastically – from its low level;
II. a phase “Os” of *oscillating* equilibria, with a strong unimodal variation in the amplitudes [h_{max} – h_{min}] and [p_{max} – p_{min}] of the oscillating densities of both host and parasite, and a parallel (but comparatively slight) unimodal variation in the periodicity of oscillation cycles;
III. a phase “S_2” of *stable* equilibria, where not only the (low) density of the host but also the (low) density of the parasite both decrease monotonically with increasing own reproductive performance ‘a’ of the parasite.

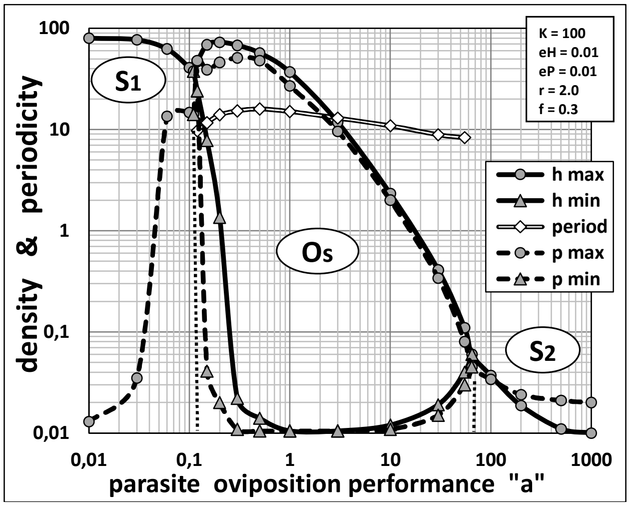

Fig. 3. Superposition of the respective patterns of density of the host [equation (11)] and the parasite [equation (12)]. ***Solid lines*****: host species;** ***dashed lines*****: parasite species;** ***fine double line*****: periodicity of cyclic oscillations (the same for both the host and the parasite)**

4. CHARACTERIZATION OF THE PHASE TRANSITIONS

The host-parasite interactions are governed by a series of factors (seven parameters in the model implemented here: see section 2), the combined influences of which can be quantified by the ratio '**π**' = [averP/averH] between the average density of the parasite and the average density of the host. As such, this ratio accounts for the intensity of the parasitism pressure against the host, a pressure which, ultimately, governs the host-parasite interactions. In this context of interacting population dynamics, the ratio **π** can be considered as playing a role which appears reminiscent and, in a way, analogous to the role played by the Gibbs' free energy in thermodynamics. Of course, this analogy should clearly be understood *only* as a *formal* analogy and, obviously, in no way implies real similarity in nature.

After this reservation has been clearly expressed, it is worth considering the extension to the ecological context of the notion of phase transition. And in particular the extension of the ancient, yet classical, approach proposed by EHRENFEST [10] as regards the classification of phase-transition categories. I therefore consider and analyze the variations – especially the derivatives – of the ratio **π** (quantifying parasitism pressure) at both phase transitions: S_1 → Os and, then, Os → S_2.

The parasitism pressure **π** is dependent upon each of all seven drivers of the host-parasite dynamics (a, f, v, for the parasite, r for the host, K, e_H, e_P for the environmental context), so that the phase transitions can be investigated along the variations of each of these seven parameters separately. Yet, the more straightforward influence on the parasite pressure **π** is, of course, the own dynamics of the parasite species itself. Accordingly, I shall focus more precisely on parameter 'a' – the mean foraging area of ovipositing parasite-females – as being the main distinctive parameter singularizing the reproductive performance of the parasite species. The case of the other parameters (f, v, r, K, e_H, e_P) will be, subsequently, briefly discussed.

Figs. 4 to 9 illustrate the variations of the ratio **π** along a large range of values of 'a', encompassing the three characteristic phases of the dynamics (S_1, Os, S_2). As the degree of parasitism pressure takes on its full meaning when considering also the own dynamics of the host, four levels of inherent rate of increase, 'r', of the host are considered: *medium* (r = 2.0: Figs. 4 & 5), *low* (r = 1.3: Fig. 6), *strong* (r = 5.0: Fig. 7) and *very strong* (r = 10.0: Fig. 8).

- at a "*low*" level of the host rate of increase, r = 1.3, the derivative (with respect to 'a') of the parasitism pressure **π** show no discontinuity, neither at the S_1 → Os, nor at the Os → S_2 phase transitions (Fig. 6).

- at a "*medium"* level of the host rate of increase, r = 2.0, the parasitism pressure **π** undergoes a *first order* phase transition at S_1 → Os (strong discontinuity of the first derivative of **π** with respect to 'a'), while the Os → S_2 phase transition remains continuous (Figs. 4 & 5).
- at *a "strong"* level of the host rate of increase, r = 5.0, the parasitism pressure undergoes a *first order* phase transition at S_1 → Os, which is still more conspicuous than at the "medium" level. At the Os → S_2 phase transition, the first derivative of **π** still remains continuous, while its second derivative rather sharply changes in sign, which might be evocative of a *second order* transition: Fig. 7.
- at *a "very strong"* level of the host rate of increase, r = 10.0, the parasitism pressure undergoes a *first order* phase transition at both the S_1 → Os and the Os → S_2 transitions, with the former transition still more conspicuous than above, while the second transition is less pronounced: Fig. 8.

The superposition of the four cases studied above (Fig. 9) clearly highlights the increasing acuteness and amplitude of the discontinuity at the phase transitions with increasing level of the own host dynamics 'r'.

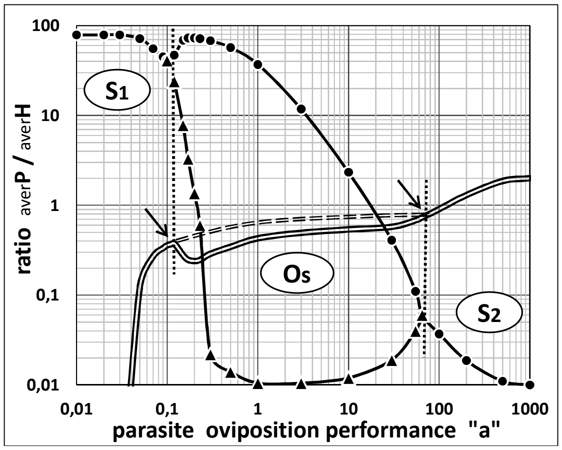

Fig. 4. The ratio π between the average parasite density and the average host density (averP / averH, quantifying the relative parasitism pressure) plotted against increasing parasite reproductive (ovipositing) performance 'a': *double line*. Note the strong discontinuity of π at the phase transition S_1 → Os and the smooth transition at the phase transition Os → S_2. The *interrupted* double line stands for *hypothetic* values of π if the oscillatory phase would not exist. [computed from equations (11) & (12) with K = 100, r = 2.0, f = 0.3, v = 1, $e_H = e_P = 0.01$]

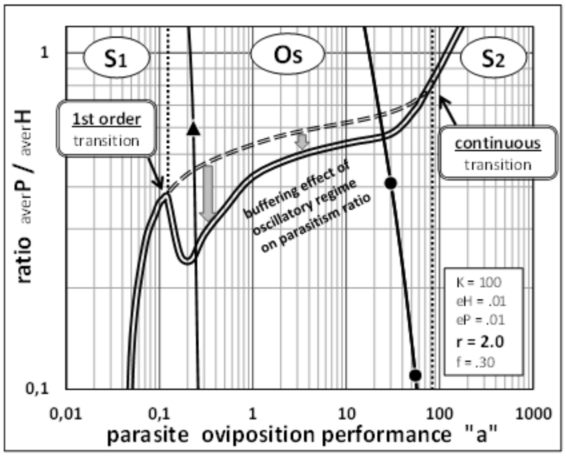

Fig. 5. Answer of the parasitism pressure π (double line) to increasing parasite reproductive (oviposition) efficiency 'a'. Computed for host inherent rate of increase: r = 2.0

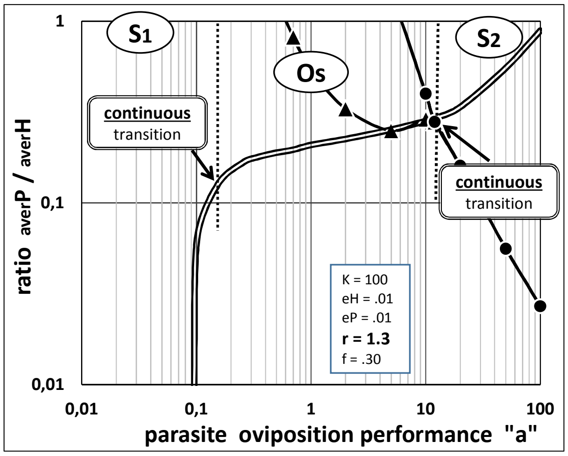

Fig. 6. Answer of the parasitism pressure π (double line) to increasing parasite reproductive (oviposition) efficiency 'a'. Computed for host inherent rate of increase: r = 1.3

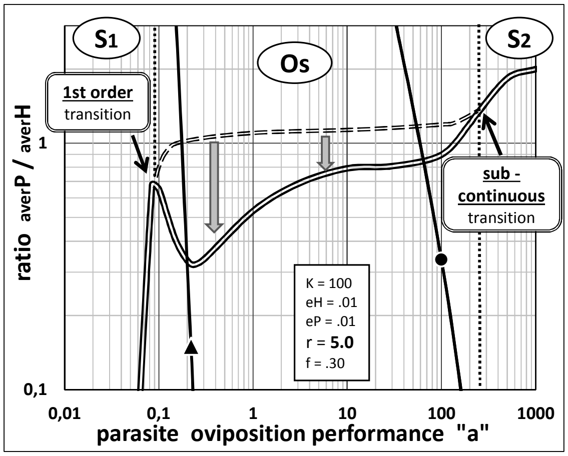

Fig. 7. Answer of the parasitism pressure π (double line) to increasing parasite reproductive (oviposition) efficiency 'a'. Computed for host inherent rate of increase: r = 5.0

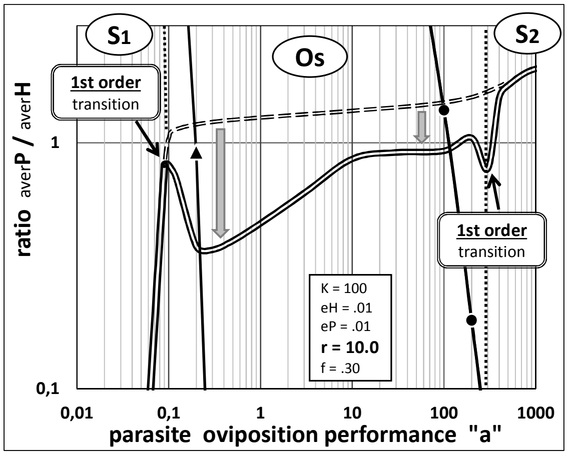

Fig. 8. Answer of the parasitism pressure π (double line) to increasing parasite reproductive (oviposition) efficiency 'a'. Computed for host inherent rate of increase: r = 10.0

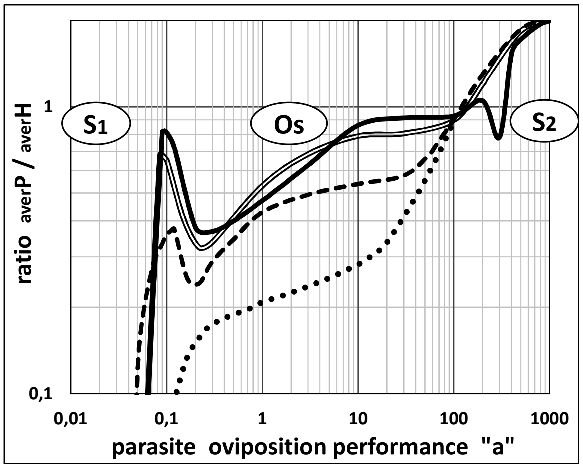

Fig. 9. The ratio π (quantifying the relative parasitism pressure) plotted against increasing parasite reproductive (oviposition) efficiency 'a' for four different values of the host reproductive efficiency 'r': r = 1.3 dotted line; r = 2.0 *dashed line*; r = 5.0 *double line*; r = 10.0 *solid line*; computed from equations (11) & (12). Note the increase of both acuteness and amplitude of the discontinuity of the parasitism pressure π with growing own-dynamics, 'r', of the host and, more generally, with increasing values reached by the parasitism pressure π just prior to the phase transition

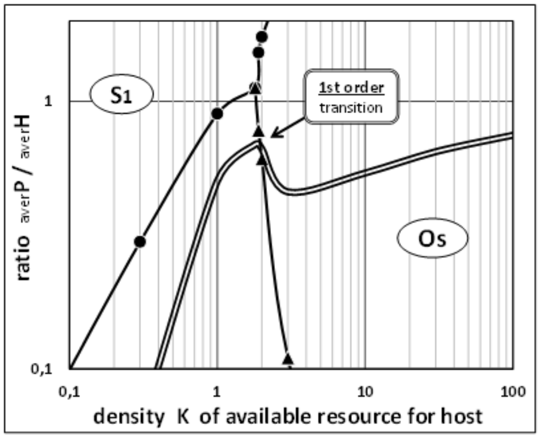

Fig. 10. The ratio π (quantifying the relative parasitism pressure) plotted against increasing density K of the available feeding resource for the host. Note the discontinuity of the first derivative of π at the phase transition S1 → Os.
[computed from equations (11) & (12) with r = 5.0, a = 5.0, f = 0.3, v = 1, $e_H = e_P = 0.01$]

More generally, the higher the level reached by the parasitism pressure **π** at the approach of the phase transition, the stronger is the following sharp decline of **π** at the transition and, accordingly, the stronger is the resulting recess of the parasitism pressure **π** all across the phase of oscillatory equilibrium (Fig. 9). Thus – as schematically shown by the grey arrows in Figs. 5, 7, 8 – entering the phase of oscillatory equilibrium results in a more or less substantial attenuation in the increase of the relative pressure of parasitism, despite the continuous increase of the own dynamics 'a' of the parasite species. And all the more so that this parasitism pressure has reached a higher value just before the transition from stable to oscillatory equilibrium. Similar trends are highlighted when considering the consequences of the variations of the parameters other than 'a', which also influence the parasitism pressure **π**, namely: *f, v, r, K,* e_H, e_P. For example, increasing the density, K, of the available feeding resource for the host generates a first-order S_1 → Os phase transition, as shown in Fig. 10.

In fact, whatever the parameter involved (a, f, v, r, K, e_H, e_P), the higher is the resulting parasitism pressure **π** at the approach of the phase transition, the more acute is this phase transition (i.e. from continuous, to second-order, to first-order).

5. DISCUSSION

The respective densities of the parasite and the host species (and more generally of predator and prey) can reach equilibrium according to two mutually exclusive modalities: either a *stable* mutual equilibrium or, alternatively, an *oscillating* regime leading to *periodic cycles* of the respective densities, with equilibrium being achieved only on average along a cycle. The amplitude of the cycles (which can often reach several orders of magnitudes for both the host and the parasite), as well as the somewhat astonishing regularity of the amplitude and periodicity of the cycles, both have elicited much attention and interest from naturalists. This very distinct equilibrium patterns either stable or oscillatory, with clear-cut transitions from one pattern to the other, have been fully *rationalized* in relation to variations of either the contextual (environmental) conditions or the varying own dynamics of the parasite or the host. This is a major outcome of having developed and implemented an *extended* version of the classical Nicholson & Bailey model.

Besides, and from a more speculative point of view, these very distinct patterns of either stable or oscillatory equilibria, with clear-cut transitions, are suggestive of the notion of *phases* and *phase-transitions*, well-known otherwise in thermodynamics. The latter point has been addressed recently, but essentially according to very general perspectives [11,12], so that a more focused analysis was still lacking, regarding (i) the nature of the phase transitions between stable and oscillatory equilibria and (ii) how this nature may possibly depend (or not) on the biological and contextual factors driving the interactive host-parasite dynamics. In turn, such a focused analysis is another outcome of the prior development of the *extended* Nicholson & Bailey model, explicitly involving the above defined *biological* factors (namely: 'a', 'f', 'v' ; 'r') and *contextual* parameters (namely: 'K', 'e_P', 'e_H'), a requirement not satisfied by the very general models that had been implemented up to now in this respect.

Several important aspects of the phase pattern and the phase-transitions, specifically relevant to the context of host-parasite dynamics, have been highlighted:

I. between the phase S_1 of stable equilibrium (at low parasitism pressure/high host density) and the phase Os of periodic oscillations,
II. between the phase Os of periodic oscillations and the phase S_2 of stable equilibrium (at high parasitism pressure/ low host density level).

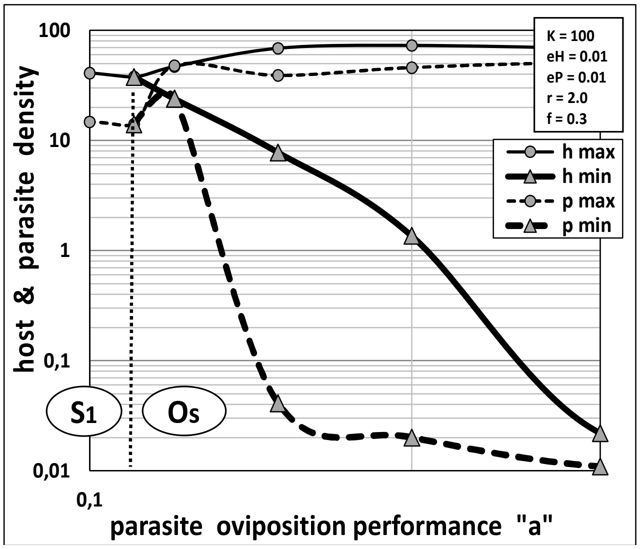

Fig. 11. Enlargement of Figure 3, focused on the phase transition S_1 → Os. Highlighted is the quite stronger breaking down of p_{min}, as compared to h_{min}

Among these interesting aspects, the following deserve being emphasized:

1. The *relative parasitism pressure* **π** (quantified as the ratio **π** between average parasite density and average host density) reveals being an appropriate parameter to characterize the type of phase transition (*sensu* EHRENFEST) – in a manner similar (in *formal* terms, not in nature, of course) to the notion of Gibbs free energy, used for analyzing thermodynamic phase transitions ;
2. There is a clear *dissymmetry* in the *sharpness* of the two phase transitions, $S_1 \rightarrow Os$ and $Os \rightarrow S_2$, with the former exhibiting a stronger degree of discontinuity of the derivative of parasitism pressure **π** than does the latter ;
3. Yet, in both cases, the *type of phase transition* can be either 1st order (discontinuous 1st derivative of **π**), 2nd order (discontinuous 2nd derivative of **π**) or more continuous;
4. For both $S_1 \rightarrow Os$ and $Os \rightarrow S_2$ phase transitions, the *sharpness of the transition* goes increasing (from continuous to 2nd order, to 1st order) with increasing level reached by the parasitism pressure **π** at the approach of the phase transition. And this stands whatever the parameter(s) – among 'a', 'f', 'v', 'r', 'K', 'e_P', 'e_H' – that are involved in the variation of the parasitism pressure.
5. Entering the phase, Os, of "oscillatory equilibrium" seems to "spontaneously" trigger a kind of negative feed-back of the parasitism pressure **π** (grey arrows in Figs. 5, 7, 8), which contribute to moderate, all along the oscillatory phase, the outcome of the "excessive" increase of the parasitism pressure **π,** reached at the end of phase S_1. This kind of "*buffering effect*" all along the phase of "oscillatory equilibrium" – well highlighted in Figs. 5, 7, 8 – can be considered as demonstrating some kind of "*relaxation oscillations*".

Interestingly, the marked discontinuity of the parasitism pressure **π** which characterizes the first order transition from stable to oscillatory equilibrium ($S1 \rightarrow Os$), is principally due to the *parasite answer* itself, when entering the "oscillatory" phase. Indeed, as shown in Figs. 3 and 11, the breaking down of the minimum density of the parasite during a cycle period is quite more severe than it is for the host. So that, it is this sudden and sharp breaking down of the parasite density during its cyclic oscillating pattern which mainly contribute to this buffering effect upon the parasitism pressure, highlighted all along the phase of "oscillatory equilibrium".

6. CONCLUSION

Physical Science in general, and Thermodynamics in particular, seem having not much to do and share – *at first sight* – with the kind of interactions that occur between parasite and host (or predator and prey) in natural ecosystems, at least in terms of *general concepts*. However, the important notion of *phase transitions*, which, at first glance, would seem more typical (or even an exclusivity) of Physics, *turns out to have suggestive extensions*, even reaching the distant realm of living world. In particular, the more or less sharp and brutal boundaries between *stable* and *strongly oscillating* equilibria, in highly interactive parasite/host or predator/prey systems, show some interesting *formal analogies* with the sharp phase transitions commonly known in thermodynamics. Such inspiring formal analogies can indeed have *true heuristic value*, as the history of Science as already provides some examples in the past.

Now, the much more modest objective and contributions of the present study have been, simply, to rationalize the connections and the quantitative dependences that actually exist, in the field, between the phase-transitions that frame the host-parasite (or prey-predator) dynamics on the one hand and, on the other hand, the relevant biological and contextual factors that drive the interactions between parasite and host, or predator and prey.

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COMPETING INTERESTS

Author has declared that no competing interests exist.

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APPENDIX

Derivation of an extended formulation of the Nicholson & Bailey model

A.1- the classical Nicholson & Bailey model

The original Nicholson & Bailey model accounts for the predator-prey interaction in discrete time and is more particularly (although not exclusively) designed to treat the parasite-host interaction in insects.

Let ‘h_i’ and ‘p_i’ be, respectively, the densities (numbers of individuals per unit area of investigation) of the host and of the parasite, at generation ‘i'. Besides – and in accordance with the Nicholson & Bailey model – it is assumed that the parasite:

I. is foraging at random for its selected kind of prey,
II. avoids oviposition upon an already egg-laid prey (or, if not so, the second oviposition does not lead to viable offspring) and
III. has some finite foraging area ‘a’.

Under these conditions, the predicted density of parasitized-host individuals complies with a Poisson distribution [5, 8].

Accordingly, the densities $h_{i,\, par}$ and $h_{i,\, non\ par}$ of parasitized and non-parasitized hots are:

$$h_{i,\, par} = h_i.(1 - \exp(- a.f.p_i)) \tag{1}$$

$$h_{i,\, non\ par} = h_i.\exp(- a.f.p_i) \tag{2}$$

with ‘f’ as the proportion of mated (and thus egg-laying) females within the whole population of parasites.

Let ‘r’ be the inherent rate of increase of the host (as it would be in the absence of any limitation in resource availability for the host development).

Accordingly, the density of hosts at generation i+1 is:

$$h_{i+1} = r.h_{i,\, non\ par} \tag{3}$$

that is:

$$h_{i+1} = r.h_i.\exp(-a.f.p_i) \quad (4)$$

The density p_{i+1} of parasites at generation i+1 is proportional to the density $h_{i,\,par}$ of parasitized hosts at generation i:

$$p_{i+1} = v.(h_{i,\,par})$$

with 'v' as the average number of viable parasite individuals issued from each parasitized host individual (proportional, in particular, to the egg clutch-size laid by ovipositing female of the parasite). The density of mated ovipositing females of the parasite at generation i+1 being, accordingly, equal to $(f.p_{i+1})$.

Accounting for the expression (1) of $h_{i,\,par}$, it comes:

$$p_{i+1} = v.h_i.(1 - \exp(-a.f.p_i)) \quad (5)$$

Note, incidentally, that equations (4) and (5) comply with the classical formalism of HASSELL: see equations (1) and (2) with m = 0 in reference [8].

A. 2 The extended Nicholson & Bailey model involving both (i) the contribution of immigration-emigration and (ii) the limitation of available feeding resource for the host

A.2.1 Immigration-emigration

Let e_H and e_P be the additional contributions (at *each* generation) of the balance between the immigration and the emigration of host (resp. parasite), in complement to the host and parasite densities computed above. It comes:

$$h_{i+1} = r.h_i.\exp(-a.f.p_i) + e_H \quad (6)$$

$$p_{i+1} = v.h_i.(1 - \exp(-a.f.p_i)) + e_P \quad (7)$$

A.2.2 Limitation of available feeding resource for the host

Moreover, let 'R' be the density of available feeding resource for the host insects (typically, for an herbivore insect, the density of leaves of the appropriate plant species, acceptable for the successful development of offspring) and 'c' the mean consummation of resource necessary to the full development of a host individual. Thus, the carrying capacity for the host insects (i.e. the density of host individuals that could be fed by the hypothetically exhaustive consummation of the available resource) is 'K', with:

$$K = R/c \quad (8)$$

The relationship between the densities of host individuals at the successive generations i and i+1, provided by equation (4) (or equation (6) accounting for immigration-emigration), should then be modified to account for the limiting carrying capacity 'K'.

The consequences of the limited availability – if any – of resource for the host depend, in particular, upon the pattern of intra-specific competition for this resource among co-occurring host individuals. Let us consider successively two extreme hypotheses in this respect.

* *According to a first – somewhat unrealistic – hypothesis*, intra-specific competition for resource among co-occurring host individuals would be ideally avoided until the threshold of complete consummation of the entire available resource is finally reached. This would imply quite a strict regular pattern of distribution of eggs (and of the subsequent pattern of distribution of offspring) among the displayed resource, so as to prevent any scramble competition to occur at any time, until all available resource is actually consumed. The corresponding behavior of ovipositing host-females – aiming at reducing at most the loss liable to intra-specific competition – would undoubtedly have some positive selective value *per se*. Yet, on the other hand, it would also require, as emphasized above, an

accurate planning *a priori* of the spatial distribution of eggs among the displayed resource, based on a prior knowledge of the diet just necessary for each future larva. And this behavior of ovipositing females would also involve, in turn, a significant cost devoted to the recognition and the avoidance of already egg-laid areas, as well as an extra time-expenditure when foraging for resource to comply efficiently with this ideal prior planning. So that it seems finally rather unlikely that such a refined behavior of ovipositing females may have developed significantly (at least apart from the specific case of explicitly territorial species). According to this hypothetical and rather unlikely behavior, the density, h_{i+1}, of host individuals at generation i+1 would simply conform to equation (6) as far as h_{i+1} remains below the carrying capacity K and, beyond, equal this capacity K.

Note also that a less drastic hypothesis, which yet implies a still rather unlikely pattern of oviposition, leads to the very classic logistic model in discrete time:

$$h_{i+1} = (r.h_{i,\text{ non par}} + e_H).[1 – (h_{i,\text{ non par}} + e_H)/K] \qquad (9)$$

which can provide oscillations of the host and parasite abundances that are not only periodic but also pseudo-periodic or even chaotic.

* *According to a second, opposite hypothesis*, the pattern of oviposition displayed by the host-females (or, as well, the pattern of the subsequent distribution of offspring) is assumed being more or less random among the displayed resource. This implies, in turn, the absence of any particular effort from host-females to avoid possible intra-specific competition for resource among co-occurring host individuals. This second hypothesis should well deserve more particular attention, as it seems more likely in most host-insects, being understood that, in some case, the field reality may be somewhat an intermediate between these two opposite hypotheses.

Assuming thus a (more or less) random distribution of eggs - and of the subsequent distribution of offspring - among the displayed resource, and considering the resulting degree of crowding in resource exploitation by host offspring, it comes, in conformity with the Poisson distribution:

$$h_{i+1} = K.[1– \exp(– (r.h_{i,\text{ non par}} + e_H)/K)] \qquad (10)$$

That is a more progressive, asymptotic approach of the saturation of resource exploitation quantified by a negative exponential – which is distinctly less brutal than is, for example the linear approach to saturation involved in the logistic model, and still less brutal, *a fortiori*, than the outcome from the first hypothesis.

Accounting for the expression (2) of $h_{i,\text{ non par}}$, it comes finally :

$$h_{i+1} = K.[1– \exp (– (r.h_i.\exp(– a.f.p_i) + e_H)/K)] \qquad (11)$$

The expression (7) of the density of mated females of parasites, p_{i+1}, remains unchanged:

$$p_{i+1} = v.h_i.(1 – \exp(– a.f.p_i)) + e_P \qquad (12)$$

In contrast with the logistic model evoked above, the present model only generates regular, non-chaotic kinds of oscillations, as a result of the more progressive approach to saturation of resource exploitation by the host. Indeed, this more regular oscillations are in better accordance with many field records.

Note that:

- In the inevitably oversimplified approach of the model, the interactive dynamics of the host-parasitoid system is governed by only *six main drivers*: **r** and **K** [both relevant to the host]; **a.f** (whatever the respective values of **a** and **f**) and **v** [both relevant to the parasite]; $\mathbf{e_H}$ and $\mathbf{e_P}$ [both dependent on the environmental biological context]. All or part of these six main drivers being, in turn, variously dependent on the abiotic environmental context (climate, etc…).
- The above equations are given in terms of the *areal* densities of the parasite (p_i), of the host (h_i) and of the available resource per host (K =R/c). Now, an alternative approach is to consider the

> respective densities of the host and the parasite relative to the *carrying capacity K*, that is to consider $h'_i = h_i/K$ and $p'_i = p_i/K$. This way may be preferred in some practical concerns, as h'_i more straightforwardly highlights the degree of damage inflict by the host to the feeding resource, as this damage is often of practical – economic or esthetic – concern.

Accordingly, equations (11) and (12) can be rewritten by replacing h_i by $K.h'_i$; p_i by $K.p'_i$; e_H by $K.e'_H$ and e_P by $K.e'_P$. It comes accordingly:

$$h'_{i+1} = 1 - \exp\left(-\left(r.h'_i.\exp(-a.f.K.p'_i) + e'_H\right)\right) \qquad (11\ \text{bis})$$

and:

$$p'_{i+1} = v.h'_i.(1 - \exp(-a.f.K.p'_i)) + e'_P \qquad (12\ \text{bis})$$

A.2.3 Dependence of immigration rates of parasite and host on the average densities of parasite and host in the meta-population context

Up to now, the immigration rates, e_H and e_P, have been considered constant along the time elapsed and the successive generations of host and parasite. In particular, no relationship has been considered, that would link the immigration rates of the parasite and the host to the corresponding densities of parasite and host in the more or less distant homologous populations. Yet, it is uncommon that the host and parasite populations are completely isolated from such more or less distant homologous populations. In this “meta-population” context, some exchanges (immigration/emigration) involving both the parasite and the host individuals likely exist between the more or less distant local populations, owing to the unavoidable partial dispersal of individuals away from their native locations. Accordingly, the net immigration rates, e_P and e_H, are expected to represent some definite fraction ‘**ε**’ of the corresponding local densities p_i and h_i of the parasite and host (or their respective averages along a cyclic period when cyclic regime actually occurs). This fraction ‘ε’ thus accounts for the relative intensity of the immigration contribution to the dynamics of the interacting host-parasite system under study. Note that, under cyclic regime, the relative contribution ε of immigration is modulated by the possible partial or even complete synchronization of cycles between the more or less distant homologous host/parasite populations. With ε decreasing with increasing synchronization and ε ultimately falling down to zero in the hypothesis of total synchronization.

Let h^*_i and p^*_i be the average values of p_i and h_i in the meta-population system (i.e. across the neighboring populations); it comes accordingly, at generation i+1:

$$e_H = \varepsilon.h^*_i \text{ and } e_P = \varepsilon.p^*_i \quad \text{or, as well,} \quad e'_H = \varepsilon.h'^*_i \text{ and } e'_P = \varepsilon.p'^*_i \qquad (13)$$

these expressions having to be introduced in equations (11), (12) or (11bis), (12bis) respectively. Of course, the value of ‘ε’ may possibly differ for the host and for the parasite species.

A.2.4 Implementing the heuristic model

In spite of its extended parts detailed above, this model remains of course an approximation of a far more complex reality. Yet, as it is, with its additional improvements as compared to the original Nicholson and Bailey model, it offers valuable opportunities of conceptual, speculative investigations and, thereby, may serve as a convenient “*heuristic*” tool, designed to highlight some influential trends regarding how the interacting dynamics of the host/parasite system actually answers various modifications in the driving parameters (‘a’, ‘f’, ‘v’, ‘r’, ‘K’, ‘e_P’, ‘e_H’) of this dynamics.

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