THE REMARKABLY LOW LEAF-SELECTIVITY PRIOR TO OVIPOSITION IN THE MOTH-PEST *CAMERARIA OHRIDELLA* IS NOT UNIQUE TO THIS SPECIES WITHIN THE GENUS *CAMERARIA*

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RÉSUMÉ. — *La remarquable sélectivité de feuille avant la ponte chez le papillon* Cameraria ohridella *n'est pas propre à cette espèce dans le genre* Cameraria. — *Cameraria ohridella*, microlépidoptère dont les chenilles minent les feuilles du Marronnier *Aesculus hippocastanum,* se révèle un envahisseur persistant et tenace depuis son apparition en Europe, il y a une trentaine d'années. Ses niveaux d'incidence, ordinairement très élevés, contrastent avec ceux, bien plus modérés, rencontrés chez d'autres espèces du genre *Cameraria*. Ainsi, par exemple, *C.* gr. *guttifinitella* est cité avec une incidence plus faible de près de deux ordres de grandeurs sur les feuilles de son hôte, *Quercus emoryi* aux Etats-Unis. La performance numérique exceptionnelle de *C. ohridella* est généralement attribuée principalement à une remarquable déficience de régulation des populations par les parasitoïdes, lesquels d'ordinaire n'affectent guère plus de quelques pour cent des populations de *C. ohridella*. Ceci étant, un autre aspect remarquable chez *C. ohridella* est la très faible sélectivité dont font les femelles pondeuses parmi les feuilles de Marronnier qui s'offrent comme support de ponte; la proportion de feuilles acceptées étant souvent voisine des 100 %. Cette faible sélectivité est évidemment de nature à apporter une contribution supplémentaire au succès numérique de *C. ohridella*. Cette faible sélectivité pour les supports de ponte est-elle également une caractéristique distinctive de l'espèce au sein du genre *Cameraria*? Ou bien au contraire, d'autres espèces du genre, telle *C.* gr. *guttifinitella*, présentent-elles aussi des exigences sélectives faibles vis-à-vis de leur support de ponte? L'estimation du degré de sélectivité ("ratio d'acceptabilité des feuilles α") n'étant, en général, pratiquement pas réalisable à partir des données brutes de terrain, on fait par conséquent usage ici d'une méthode d'inférence indirecte du ratio d'acceptabilité (résumée en Annexe). On montre alors que les proportions de feuilles (respectivement de *Aesculus* et *Quercus*) que *C. ohridella* et *C.* gr. *guttifinitella* considèrent comme potentiellement acceptables sont relativement voisines et élevées (96 % et 78 %) alors que les incidences (proportions de feuilles effectivement acceptées c'est-à-dire minées) diffèrent, comme on l'a dit, de près de deux ordres de grandeur (89 % et 2 % respectivement) entre les deux espèces de *Cameraria*. Un faible niveau de sélectivité parmi les feuilles, sites potentiels de ponte, ne semble donc pas spécifique à l'espèce *C. ohridella*. Ce résultat ne fait dès lors que renforcer le bien-fondé des études visant à restaurer le niveau de régulation des populations envahissantes de *C. ohridella* par une meilleure efficience de la prédation, notamment via parasitoïdes.

SUMMARY. — *Cameraria ohridella*, a recent leaf-mining invader of the horse-chestnut tree *Aesculus hippocastanum*, likely persists as a strong pest with unusually high levels of incidence. For example, among *Cameraria* moths, *C. ohridella* ordinarily features more than hundred times denser upon *Aesculus* leaflets than *C.* gr. *guttifinitella* is upon leaves of *Quercus emoryi*. There is general agreement to consider that the singular success of *C. ohridella* in mining *Aesculus* leaves mainly results from deficient top-down control, especially extremely low level of parasitoids efficiency. Another remarkable aspect of *C. ohridella* outbreaks however is the very high level of leaves acceptance (low selectivity) of females prior to egg-laying, which may often rise up near to 100 %. Would this low bottom-up control also feature (or not) as a specificity of this species within the genus *Cameraria*? Using an appropriate indirect method, it is shown that the proportions of "*acceptable*" leaves by ovipositing females are substantially similar (and high) in both *Cameraria* species (96 % and 78 % for *Cameraria ohridella* and *C.* gr. *guttifinitella* respectively), in spite of the dramatically different proportions of "*accepted*" (= actually oviposited) leaves (89 % and 2 % respectively). In turn, this would contribute to make still more relevant the currently oriented focus upon top-down regulation as one of the major lever for a better control of *Cameraria ohridella*.

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Since a few years, the leaf-miner *Cameraria ohridella* Deschka & Dimic, 1986 (Lepidoptera: Gracillariidae), has become a true pest for horse-chestnut trees (*Aesculus hippocastanum* L.) all over Europe (Csoka, 1999; Marchesini *et al.,* 2002; Kenis *et al.,* 2005). Not only most of *Aesculus* trees are concerned now but, still further, each one is ordinarily quite heavily affected. Indeed, such a strong invasion really differs from the situation prevailing for most of other leaf-miners which usually subsist in obviously more controlled populations, even those which, like *Cameraria ohridella*, are recent invaders. For example, *Parectopa robiniella* remains at comparatively quite low levels of occurrence (Csoka, 1999).

Insufficient regulations of larval development from either top-down or bottom-up contributions (in particular, either a reduced level of predation or too weak plant defences against herbivores, respectively) may *a priori* contribute to explain the sustained high developmental success in strongly invasive herbivore insects such as *Cameraria ohridella*. As other leaf-mining species, including some *Cameraria* sp., obviously show highly regulated natural populations (Kenis *et al.,* 2005), it would be of both speculative and practical interest to investigate, in those strongly controlled species, whether such regulations predominantly proceed from either top-down or bottom-up sources of developmental control of their populations. Actually, *Cameraria ohridella* has already been compared to more or less closely related species, regarding the relative efficiency of top-down constraints, especially parasitoids (Grabenweger, 2004). In particular, another species of *Cameraria*, *C.* gr. *guttifinitella,* a leaf-miner upon *Quercus emoryi*, was sufficiently thoroughly investigated in the field to demonstrate a remarkably severe level of global control of its natural populations (Bultman & Faeth, 1986).

Thus, while *C. ohridella* populations typically show average densities of several individuals (typically as high as half a dozen) per leaflet upon horse-chestnut trees, the density, for *C.* gr. *guttifinitella*, averages no more than 0.02 mine per leaf, a difference of more than two orders of magnitude!

It is generally admitted that abnormally low top-down pressure (from parasitoids, predators, etc.) is the main cause for the repeatedly strong outbreaks of *Cameraria ohridella* (Marchesini *et al.,* 2002; Kenis *et al.,* 2005). Actually, parasitism levels in *C. ohridella* are currently comprised between 3 % and 10 % only (Del-Bene & Gargani, 2004; Péré & Kenis, 2006) or even less than 2-3 % (Boisneau *et al.,* 2004; Volter, 2004). For this reason probably, the role of bottom-up regulation as a possible complementary contribution to population control has received less attention. Accordingly, we shall address specifically this topic. We will especially focus upon one specific question: would the comparatively quite lower incidence of *C.* gr. *guttifinitella* result - at least in part - from a significantly stronger selectivity for leaves of mothers prior to oviposition than it is the case in *C. ohridella*?

Insects are capable of distinctly selecting among leaves (including within a same tree, within a same branch, upon a same shoot) according to a lot of either morphological, anatomical and/or biochemical factors (Kozlov & Koricheva, 1991; Gripenberg, 2007). Here, one possible reason could be, for example, that *Quercus* leaves might hypothetically oppose more efficient deterrents against larval herbivory than *Aesculus* leaflets.

In short, by comparing this way *Cameraria* gr. *guttifinitella* and *Cameraria ohridella*, we would like to assess whether or not the invasive success of the latter might be attributable, for any part, to an exceptionally low level of leaf-selectivity of females, prior to oviposition, in *C. ohridella*. A low selectivity that would possibly result from an unusually large tolerance of mining larvae regarding the nutritive quality and chemical defences of *Aesculus* leaves. Behind this speculative questioning comes, of course, the practical concern of whether or not deliberate bottom-up actions might also be worth considering or not, as a complement contribution to the major, top-down, regulation by parasitoid insects.

In this perspective, if *C. guttifinitella* would not reveal substantially more selective for leaves quality (i.e. not significantly more bottom-up controlled) than *C. ohridella*, this would likely suggest that, within this *Cameraria* group, the primarily efficient regulation source (if not the sole) would definitely be restricted to top-down mechanisms. Accordingly, we shall address this question in the following.

METHODS

As mentioned, in the present context, bottom-up regulation particularly involves the capability for host-leaves to discourage the propensity of females to lay eggs upon them. Accordingly, the relevant parameter which would properly testify for the bottom-up regulation originating from the host-plant is the proportion α of leaves that would seem *acceptable* to the "eyes" of females (Roslin *et al.* 2006). "Acceptable" leaves are those leaves which, being visited by gravid females, would then actually be accepted for the deposit of a clutch of eggs (whatever the detailed characteristics of the leaf which are decisive for the insect). Now, generally speaking, not all *acceptable* leaves will be actually *accepted,* since all of them may not be effectively visited and consequently egg-laid, depending on females' density and resulting oviposition pressure. Thus, in a practical scope, the proportion of *actually accepted* leaves, in spite of being of more direct and easy access in practice in the field, cannot at all serve as a surrogate to the estimation of the proportion α of *acceptable* leaves. As argued above, the proportion of *accepted* leaves obviously underestimate indefinably the proportion α of *acceptable* leaves. As the latter is clearly the relevant parameter in terms of behavioural relationship between the insect and the host (while the accepted proportion depends also, statistically, upon the average density of females), the proportion α is well the subject to focus upon. Accordingly, it will then be necessary to develop and implement a specific model, designed to rely the proportion α to more easily collected field data, namely the recorded distribution of eggs number per leaf. Note that the same difficulty stands up for the estimation of the clutch-size n_c, whenever the latter appears not easily accessible in the field, which is often the case with tiny insects, easily disturbed and reluctant to accept accurate observation of their activity in the field. Unfortunately, the (more easily recorded) total number of deposited eggs per leaf (i) has no straightforward behavioural significance (it also depends on gravid females' density) and (ii) cannot serve as a surrogate for the behaviour-relevant clutch-size, since it is obviously an undefined overestimate of clutch-size (several successive visits and resulting egg-clutches deposits may occur on a same acceptable leaf, from either the same or several females).

Then a specific model (see Appendix and supplementary details in Béguinot, 2005) allows the proportion of acceptable leaves (or "ratio of leaf acceptance") α to be derived from the clutch-size n_c and the easily recorded distribution of the total number of eggs per leaf issued from a representative sample of leaves.

When n_c itself cannot easily be recorded directly in the field, as is the case here, the model provides an alternative, adapted procedure through co-estimations of both α and n_c. As shown in Appendix, this procedure consists in testing iteratively a series of hypothetical values for the couple (α, n_c) for conformity of the corresponding, computed distribution of the number of eggs per leaf to the genuine field-recorded distribution. The degree of conformity is measured using the conventional least-squares method. The couple (α, n_c) which, ultimately, yields the best fit between computed and real distributions is selected as the best estimate for acceptance ratio α and clutch-size n_c.

In practice here, as eggs are not so easy to be detected reliably upon leaves, we shall subsequently use data issued from counting mines rather than from eggs occurrence. Accordingly, here, n_c must be understood not as the average size of eggs-clutch but as the average size of the resulting '*mines-clutch*', which may notably differ from the former by the proportion of non-hatched eggs. Regarding acceptance ratio α, it can be immediately verified (see Appendix) that, by construction, its computed estimation remains unaffected when moving from eggs-census to mines-census.

The distribution of the number of mines per leaf in *Cameraria ohridella* was obtained from representative samples (135, 163 and 257 leaflets of horse-chestnut respectively) at three sites, in the north and central part of France (Lagny, east of Paris; Chalon-sur-Saône and Le Creusot in southern Burgundy).

For *C.* gr. *guttifinitella,* which mines the leaves of *Quercus emoryi*, we make use of the data published by Bultman and Faeth (1986: table 3) which involve a considerable set of material (100 236 leaves among which 2040 are mined by *C.* gr. *guttifinitella).*

RESULTS

The joint estimation (n_c, α) of the clutch-size n_c and the leaf-acceptability ratio α is obtained (as already mentioned) by seeking for the best fit between observed and computed data (namely the distribution of the number of eggs or resulting mines per leaf) for varied hypothetical values of n_c and α, using the least-squares method to assess the goodness of fit (Fig. 1).

The values of (n_c, α) are given in Table I, which summarizes the four main factors relevant to the question under analysis, namely:

- as *inferred* "causes", the values of 'behavioural parameters' α and n_c computed according to the model mentioned above;

- as *observed* "results", the recorded proportion β of mined leaves and, eventually, the exploitation ratio of acceptable leaves (β/α).

Both *Cameraria ohridella* and *Cameraria* gr. *guttifinitella* show fairly similar figures as to the proportion α of acceptable leaves for oviposition but strongly contrasted ratios of exploitation of the latter for oviposition (Fig. 2).
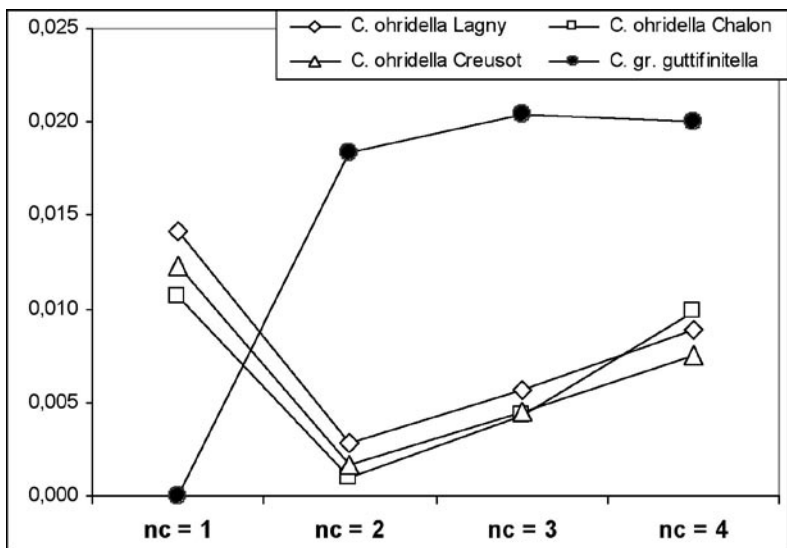
Figure 1. — The average distance (as the relative sum-of-squares) between the observed distribution of the number of mines per leaflet and the corresponding computed distribution for different hypothetical values of n_c. The best fit suggests $n_c = 2$ for *C. ohridella* and $n_c = 1$ for *C.* gr. *guttifinitella*.
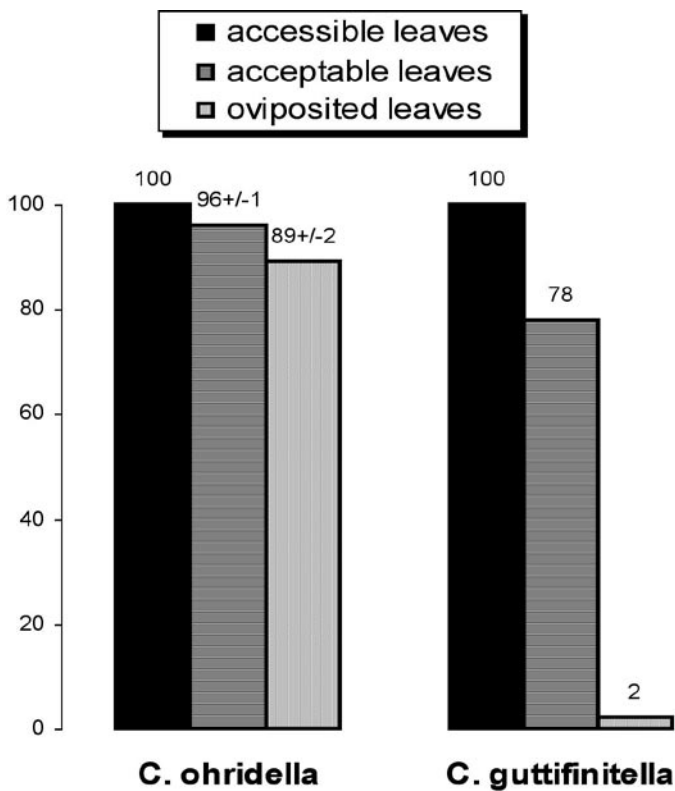

Figure 2. — Among 100 *accessible* leaves, number of *acceptable* leaves (= $100.\alpha$) and among the latter, number of actually *oviposited* leaves (= $100.\beta$) (NB: for *C. ohridella* , average of 3 samples).

TABLE 1

Inferred values for 'behavioural parameters' α and n_c; recorded level β of leaf-mining incidence and the resulting ratio of exploitation (β/α) of the potentially acceptable leaves (for Quercus*) or leaflets of compound leaves (for* Aesculus*)*

leaf-mining species	α: computed proportion of «acceptable» supports	n_c computed size of mines-clutch	β: recorded proportion of affected (= mined) leaflets (resp. leaves)	exploitation ratio of acceptable leaflets or leaves (β/α)
C. ohridella Lagny	97%	2	87%	90%
C. ohridella Chalon/S	95%	2	88%	93%
C. ohridella Le Creusot	97%	2	91%	94%
C. gr. *guttifinitella*	78%	1	2.0%	2.6%

DISCUSSION

Quite schematically, the level of developmental success of a population of herbivores is dependent upon four main factors: (i) the own 'intrinsic' performance of the herbivore species itself (fecundity, etc.), subsequently modulated by (ii) bottom-up and (iii) top-down constraints, to which should be added (iv) environmental influences such as plant-hosts dispersion and their accessibility to the herbivores.

We focus here on point (ii) and, more specifically, on the level of *leaf acceptance by laying females* α**,** a behavioural parameter which would logically decrease as a direct answer to increasing constraints that plant may oppose to the optimal development of larvae, at least, as far as the "preference-performance" hypothesis remains sound here (Awmack & Leather, 2002; Babendreier & Hoffmeister, 2002; Bultman & Faeth, 1986; Craig *et al.,* 1989; Heisswolf *et al.,* 2005; Hódar *et al.,* 2002; Jaenike, 1978; Thompson & Pellmyr, 1991; Waltz & Whitham, 1997; but see also Eber, 2004; Scheirs *et al.,* 2002; Valladares & Lawton, 1991).

The (here) undifferentiated, cumulated contributions of the other three main factors are then liable to be appreciated by difference.

Considering the high recorded proportion of mined leaves (89 % ± 2 %), the high level of leaf-acceptance α of *C. ohridella* (α = 96 % ± 1 %), is of course not a surprise. On the contrary, a high level of leaf acceptance (α = 78 %) also for *C.* gr. *guttifinitella* makes a clear contrast with the remarkably low density of leaves actually mined by this species. Accordingly, the exploitation pressure upon acceptable leaves, which is next to saturation (90 %) for *C. ohridella*, remains comparatively very weak for *C.* gr. *guttifinitella* (2.6%, i.e. 35 times lesser). Thus, the exceptionally high density of leaves mined by *C. ohridella* on *Aesculus*, more than 40 times greater than for *C.* gr. *guttifinitella* on *Quercus* (89 % vs 2 %), may primarily be attributable to the proportionally stronger contributions of one or several intrinsic, environmental and top-down contributions to the regulation of populations of *C.* gr. *guttifinitella*. This statement once more is not a surprise but now there is the supplementary information that a high level of leaf-acceptance prior to egg-laying like that in *C. ohridella* does not feature unique within the genus *Cameraria* but does not necessarily imply a high developmental success of the species, as demonstrated here by *C.* gr. *guttifinitella*.

These shared high levels of leaf-acceptance suggest that *Cameraria* moths (at least these two species) have fairly well overcome the defences that hosts-plants have elaborated against insect herbivory. Indeed, turning away the multiple sources of defence from the host-plant, among which are, (i) variable quality of intra-foliar nutritive resources (Cowles, 2004; Dajoz, 1993; Eber, 2004; Feeny, 1970; Heisswolf *et al.,* 2005; Murakami *et al.,* 2005; Scheirs *et al.*, 2001; Whitham, 1992) and also, (ii) a series of noxious deterrents (Feeny, 1970; Harribal & Feeny, 2003; Lill & Marquis, 2001; Murakami *et al.,* 2005; Whitham 1992), is certainly a decisive contribution to herbivorous insects' success.

Thus, the evident low bottom-up control in *Cameraria ohridella* might, in fact, be a shared and stable character across all or part of the genus *Cameraria*, perhaps in relation to the rela-

tively long sap-feeding period within larval development course in *Cameraria* (Needham *et al*., 1928), which would proportionally reduce the proportion of ingested deterrents-rich foliar tissues; and this would accordingly dismiss any hope of natural evolution towards an increase of bottom-up regulation. On the contrary, this would contribute to assign still more relevance to the currently oriented focus upon top-down regulation as the major source for a better control of *Cameraria ohridella*.

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APPENDIX
A BRIEF DESCRIPTION OF THE 'MELBA' PROCEDURE
("MULTI-EGG-LAYING BEHAVIOUR ANALYSIS; MORE DETAILS IN BÉGUINOT, 2005)

ASSUMPTIONS INVOLVED IN THE MODEL

Let consider a stand of n_u potential host-units among which an unknown proportion α is acceptable by the mothers (gravid females), i.e. has the sufficient level of quality for females taking the decision of egg-laying on them. Let **v** be the number of "efficient" visits (concluded by deposition of a clutch of eggs) received by a given acceptable host-unit. We admit:

(i) that these visits are distributed *randomly* among *acceptable* host-units (but of course non-randomly among *all* units), an assumption fairly admissible and commonly referred to (Sugimoto, 1980: 15; Connor *et al.,* 1997; Kuhlmann *et al.,* 1998; Wool & Ben-Zvi, 1998; Kagata & Ohgushi, 2002; Vos & Hemerik, 2003; Ives & Godfray, 2006);

(ii) that differences which may subsist between acceptable host-units, in terms of probability of visit by mothers and clutch-size decision when ovipositing upon, might be neglected as a first approximation since these host-units belong to the *same type*, or same 'space unit' from the insect point of view (Kuczynski & Skoracka, 2005) with more or less similar sizes. Such simplifications are commonly used in models, see for example, Kagata & Ohgushi (2004) for leaf-miners or Kuczynski & Skoracka (2005) for leaf-gallers;

(iii) to consider *those species only* for which mothers *do not* decidedly avoid nor restrict oviposition upon units already visited previously by themselves or conspecifics (Auerbach & Simberloff, 1989; Kagata & Ohgushi, 2002; Cornelissen & Stiling, 2006; Gripenberg *et al*., 2007). In particular should be excluded from the procedure those cases where the distribution of the recorded numbers of eggs per acceptable unit would show a variance sub-null or, at least, much lower than the mean, especially when females density and oviposition pressure are high, since that would suggest avoidance of multiplicative egg-laying' bouts on a same unit.

NB: this last condition, having *not* a general applicability, has therefore to be verified specifically before implementing the procedure. Here, this was positively verified for both *Cameraria* species.

THE MODEL

Accordingly, under these assumptions, the number **v** of (efficient) visits received per *acceptable* host-units is distributed in accordance with the Poisson law. Let then $\Pi(v)$ be the proportion of units that received v efficient visits, across the *whole set* of **n_u** potential host-units (i.e. $\Pi(v)$ is the distribution of the number v of efficient visits per unit, among the *whole set* of units).

For $v \neq 0$, only the acceptable units are concerned by definition. Then, $\Pi(v)$ is given by applying the Poisson law to the set of *acceptable* host-units only, which is in proportion α. Accordingly, its contribution should involve Poisson expression multiplied by α:

$\Pi(v) = \alpha \cdot \exp(-\mu) \cdot \mu^v / v!$ [**1**] *(for v ≠ 0)*

For $v = 0$, two components are involved: all the non-acceptable units (proportion $(1 - \alpha)$) and also those acceptable units that, by chance, have received no visit:

$\Pi(v) = 1 - \alpha + \alpha \cdot \exp(-\mu)$ [**1'**] *(for v = 0)*

with **μ** as the average number of *"efficient"* (concluded by egg-laying) visits received per acceptable unit.

Now, what may be observed and quoted *a posteriori* is not the number of efficient visits per unit but their direct material consequences in terms of the number η per host-unit of either deposited eggs or resulting "artefacts" such as mines or galls (the 'recorded objects').

Let then **n_c** be the clutch-size, applying to the chosen recorded objects.

If *deposited eggs* are the recordable objects in the field, then **n_c** corresponds to the usual definition of clutch size: the number of eggs deposited in a single bout.

If *resulting artefacts* (mines, galls,…) are now the recorded objects, then **n_c** will be the average number of these 'residual' artefacts resulting from one clutch of eggs; in this case **n_c** (the 'residual' clutch-size) might be lower than the egg clutch size itself, depending on the ratio of developmental success of eggs.

Accordingly, the model will permit inferring the clutch-size *strictly* speaking only if *eggs* might be numbered; conversely, if only resulting *artefacts* are recordable, the model will merely provide the size of the '*residual* clutch' applying to artefacts (unless correction may be applied from previous knowledge of the hatching ratio of eggs, which will generally not be the case).

The number η of eggs/artefacts per unit is thus $\eta = v.n_c$, with n_c being either the 'eggs' or the 'artefacts' clutch-size. The distribution $\Pi(\eta)$ of the number of eggs/artefacts per unit, among the whole sample of n_u host-units, is therefore computed by simply substituting v by η/n_c, in equations [**1**] & [**1'**]:

* for any full positive values of (η/n_c), i.e. for acceptable units that were visited at least once:

$$\Pi(\eta) = \alpha.\exp(-\mu).\mu^{(\eta/nc)}/(\eta/n_c)! \quad [\mathbf{2}]$$

* and for $\eta = 0$:

$$\Pi(0) = 1 - \alpha + \alpha.\exp(-\mu) \quad [\mathbf{2'}]$$

The average number **μ** of *"efficient"* visits per acceptable unit is given by $\mu = (n_e/n_c)/(\alpha.n_u) = n_e/(\alpha.n_c.n_u)$ with n_e as the total number of eggs (or total number of resulting artefacts: mines/galls) within the whole studied sample of n_u potential host-units (acceptable or not) [note that considering either eggs or associated artefacts does not modify (n_e/n_c) nor μ, since, correspondingly, n_c is the clutch-size applied to either eggs or their resulting artefacts. Therefore, the acceptance ratio α also remains unchanged since $\alpha = (n_e/n_c)/(\mu.n_u)$].

Now, the estimation of both **n_c** and α is obtained by comparing the field-recorded distribution $\Pi(\eta)$ (established for either eggs or their resulting artefacts) to the corresponding computed distribution $\Pi(\eta)$.

In practice, this estimation is obtained iteratively, seeking for the set of values $\{$**n_c** & $\alpha\}$ which leads to the best fit between *field-recorded* and *computed* distributions $\Pi(\eta)$, being well understood that, as already mentioned, n_c corresponds either to the eggs' or to the mines/galls' clutch-size.

NB: in practice, each clutch of eggs may somewhat vary in size around its average value n_c; this is the reason why, actually, the observed $\Pi(\eta)$ are generally more or less a continuous function of η, i.e. with non-zero values not restricted *only* to the multiples of n_c. To account for this in the model and thus keep closer to reality, a limited range of fluctuation of clutch size, around its average value n_c, is introduced in the model (for practical details on this point, see Béguinot, 2005).