LMC and MVT match together
Work no longer in progress

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on an idea of Éric Wajnberg

december, 15, 2009

Abstract

Éric Wajnberg asked how to consider simultaneously both the optimal sex ratio (according to Hamilton's Local Mate Competition formalism, [Ham67]) and the optimal patch time allocation (according to Charnov's optimal foraging formalism, [Cha76]) for the same egg laying parasitoid. The answer is obtained, as in LMC, by looking for a Wardrop equlibrium in terms of the number of mutant genes in the second generation offspring, but, as in the MVT, taking into account the time used in harvesting a patch of hosts, with a decreasing effciency due to patch depletion, to optimize a lifetime count.

The unexpected (?) result is that both Hamilton's LMC and Charnov's MVT results hold unchanged. While we bundle the two problems in a single one involving both "decisions", the result uncouples them.

We also look for a credible time behaviour of the parasitoids that implements these optimal strategies with minimal "knowledge" of the scenario.

1 Introduction

In some sense, the two emblematic problems of behavioural ecology are the stable sex determination in Hamilton's *Local Mate Competition* [Ham67] and the optimal patch residence time dominated by Charnov's Marginal Value Theorem [Cha76]. Many authors have in various ways combined the two problems. Among them, Waage and co-authors [WL84, WN84, Waa86], and more recently Nagelkerke [Nag94] and Nagelkerke, van Baalen and Sabelis [NvBS96].

In contrast to these last two references, the rationale for optimizing clutch size here is the decreasing efficiency of the foraging activity due to patch depletion as the clutch size grows, forcing a trade-off, in time limited parasitoids, between the time lost in foraging a depleted patch on the one hand, and in searching for a new patch of hosts upon leaving a depleted one on the other hand. This also leads us to consider patches of variying qualities, making this quality, q, and the number n of females foraging the same patch the two parameters of any scenario.

However, we do not consider the effect of the total clutch size on the competition for food in the offspring, the main factor in these references.

2 The global, or "ultimate" problem

2.1 Matching LMC and optimal foraging

We consider a mutant parasitoid laying eggs in a patch of hosts where $n-1$ other natural conspecifics are also parasitizing. The *quality* of the patch is the number q of hosts it holds. Following a question raised by Éric Wajnberg, we are interested in both its time t spent on the patch and the sex ration r of its clutch.

In the classical MVT approach, one takes the time t spent on the patch as the parameter to optimize, and considers the resulting number of eggs layed, or clutch size c, say $c = f(n,q,t)$. Here, for several reasons, we have rather use the clutch size c as the independant variable, and consider the reciprocal function $t = g(n,q,c)$ giving the time spent as a function of n, q and c. We do not assume any specific form for g. It may take into account any degree of interference between the foragers as deemed necessary.

The approach of the MVT [Cha76] seeks to account for the lifetime egg number by assuming that the behaviour of the parasitoid is approximately age independant, so that this count is proportional to the number of eggs layed per unit time. We shall use that approximation for both the generation of the focal parasitoid and the next generation. To do so, we need the average search time T between two patches.

Notice that c may be a function of n and q. Both n and q vary in the environment. We shall use the terminology of random variables to represent their distribution. As a result a "choice" of behaviour $c(n,q)$ will turn c into a random variable.

Both n and q are (bounded) integers. Hence only a finite number of combinations (n,q) are possible. Let us number the couples present in the environement as $\{(n_k,q_k)\}$, and their relative frequencies, or probabilities of beeing met, as p_k, $k=1,\ldots,K$. We shall use the notation $g(n_k,q_k,c) = g_k(c)$, and for any feedback law $c(n,q)$, we shall likewise let $c_k := c(n_k,q_k)$. Let also the weighted mean values, or expectations, be denoted as $\bar{c}$ and $\bar{g}$. Likewise, a choice of behaviour $r(n,q)$ will make the mutant's sex ratio into a random variable denoted $r_k = r(n_k,q_k)$.

The incumbent, "natural" population is assumed to use a law $c^\star(n,q)$ with mean value $\bar{c}^\star$ and mean time spent on a patch $\bar{g}^\star$, and a male ratio $r^\star(n,q)$.

We compute the number of mutated genes in the second generation using Hamilton's method [Ham67], except that to account for a lifetime count, we consider at each generation the number of offspring *per unit time*. (The total numbers would therefore be obtained by multiplying through by the square of the (average) life time of the prasitoids.) We obtain a yield Y for the mutant population:

$$\begin{aligned} Y = \frac{1}{T+\bar g}\mathbb{E}\Bigg[& c(1-r)\frac{\bar c}{T+\bar g}+ \\ & \left(c(1-r)\frac{\bar c}{T+\bar g}+(n-1)c^\star(1-r^\star)\frac{\bar c^\star}{T+\bar g^\star}\right)\frac{cr}{cr+(n-1)c^\star r^\star}\Bigg]. \end{aligned} \tag{1}$$

Observe that, if $c=c^\star$ and $r=r^\star$, this results in $Y=Y^\star$ with

$$Y^\star = \frac{2(\bar c^\star)^2(1-r^\star)}{(T+\bar g^\star)^2}$$

It is also of interest to consider the mean egg-laying rate of the parasitoids $X^\star$ in the same case:

$$X^\star = \frac{\bar c^\star}{T+\bar g^\star} = \frac{T+\bar g^\star}{2\bar c^\star(1-\bar r^\star)}Y^\star\,. \tag{2}$$

If there is an ESS, it first has to be a Wardrop equilibrium, i.e. the choice $c=c^\star$ and $r=r^\star$ should be optimal. We will investigate the first order conditions for this to happen. Since both c and r are functions of n and q this must be done with some care. In particular, the effect of a variation of these functions on their means must be dealt with.

In that respect, for any function $\varphi(c,r,g,\bar c,\bar g)$, using a sub index k to mean that the arguments are $(c_k,r_k,g(q_k,c_k),\bar c,\bar g)$ and denoting g' the partial $\partial g/\partial c$, we have:

$$\frac{\partial\mathbb{E}\varphi}{\partial c_i} = p_i\left[\frac{\partial\varphi_i}{\partial c_i}+\frac{\partial\varphi_i}{\partial g}g'_i+\sum_k p_k\left(\frac{\partial\varphi_k}{\partial\bar c}+\frac{\partial\varphi_k}{\partial\bar g}g'_i\right)\right].$$

2.2 Optimizing c

Applying the above formua to Y in (1) above, it yields

$$\begin{aligned} \frac{T+\bar g}{p_i}\frac{\partial Y}{\partial c_i} = -g'_iY+\frac{(1-r_i)\bar c}{T+\bar g}\left(1+\frac{c_ir_i}{c_ir_i+(n-1)c_i^\star r_i^\star}\right)+ \\ \frac{c_i(1-r_i)\bar c+(n-1)c_i^\star(1-r_i^\star)\bar c^\star}{T+\bar g}\times\frac{(n-1)r_ic_i^\star r_i^\star}{(c_ir_i+(n-1)c_i^\star r_i^\star]^2}+ \\ \frac{1}{T+\bar g}\sum_k p_kc_k(1-r_k)\left(1-\frac{\bar c g'_i}{T+\bar g}\right)\left(1+\frac{c_kr_k}{c_kr_k+(n-1)C_k^\star r_k^\star}\right). \end{aligned}$$

Set all variables to their "star" value and equate to zero, to obtain

$$0 = -g_i' Y^\star + 2\frac{(1-r_i^\star)\bar{c}^\star}{T+\bar{g}^\star} + \frac{1}{T+\bar{g}^\star}\sum_k p_k \frac{n+1}{n} c_k^\star (1-r_k^\star)\left(1-\frac{\bar{c}}{T+\bar{g}} g_i'\right),$$

or, multiplying everything again by $(T+\bar{g}^\star)$ and taking (2) into account

$$0 = -2(1-r_i^\star)\bar{c}^\star(1-g_i'X^\star) + \sum_k p_k \frac{n+1}{n} c_k^\star (1-r_k^\star)(1-X^\star g_i').$$

It follows that the choice $g_i' = 1/X^\star$ anihilates the partial derivative, or, going back to the classical function $f(n,q,t)$ which is the inverse function of g, and for all couples (n,q) present in the environment

$$\frac{\partial f(n,q,t)}{\partial t} = X^\star\,. \tag{3}$$

This is exactly Charnov's formula or the M.V.T. [Cha76]

2.3 Optimizing r

We now differentiate (1) with respect to r_i:

$$\frac{T+\bar{g}}{p_i}\frac{\partial Y}{\partial r_i} = -\frac{c_i\bar{c}}{T+\bar{g}}\left(1+\frac{c_i r_i}{c_i r_i + (n-1)c_i^\star r_i^\star}\right) + \left[c_i(1-r_i)\frac{\bar{c}}{T+\bar{g}} + (n-1)c_i^\star(1-r_i^\star)\frac{\bar{c}^\star}{T+\bar{g}^\star}\right]\frac{c_i(n-1)c_i^\star r_i^\star}{[c_i r_i + (n-1)C_i^\star r_i^\star]^2}.$$

Again, set all variables to their star value, multiply everything by $(T+\bar{g}^\star)$ and equate to zero to obtain

$$\frac{n+1}{n} = \frac{1-r_i^\star}{r_i^\star}\frac{n-1}{n}\,,$$

or

$$r_i^\star = \frac{n-1}{2n} =: r^\star(n)$$

which is Hamilton's L.M.C. value. [Ham67]

2.4 Conclusion

The thing that hath been, it is that which shall be; and that which is done is that which shall be done: and there is no new thing under the sun [Qo940BC].

3 The proximal problem

The issue now is to find a detailed time behaviour of the parasitoid that would lead to the "ultimate" result.

Concerning the optimal foraging time, one may consider that the parasitoid just monitors the rate at which it finds healthy hosts, and leaves when that rate drops below a given threshold. This is simple enough to be a credible behaviour rule. It is independant on both the nmber n of females on a given host patch and the quality q (number of hosts) of the patch.

Concerning the male ratio, it has been suggested [WL84], verified in several species as well as by statistical simulation [Waj94] that, ignoring the variable egg laying rate due to patch depletion, the LMC result could be obtained by a "males first" strategy, also independant on both characteristics n and q of the scenario. The question thus arises of whether such a strategy can be prescribed in the combined LMC-MVT framework investigated here, taking into account patch depletion.

3.1 General case

3.1.1 Global male ratio under variable egg-laying rate

Let $\dot{c} = f'(n,q,t)$ be the egg-laying rate, and μ be the instantaneous male ratio being used by the female. The total number of males layed from time zero to t is

$$m(t) = \int_0^t \mu(s)\dot{c}(s)\,\mathrm{d}s\,.$$

Therefore, the male ratio r at time t is

$$r(t) = \frac{m(t)}{c(t)} = \frac{\int_0^t \mu(s) f'(n,q,s)\,\mathrm{d}s}{f(n,q,t)}\,.$$

3.1.2 An egg-laying strategy

Let N be a number larger than any plausible number n of parasitoids on the same patch. In that respect, one may notice that if n is close to q, the classical MVT results have no meaning, as, for $n = q$, say, the ratio of healthy hosts on the patch falls from 1 to 0 in one ovipositing sequence.

Let $t^\star_{n,q}$ be the optimal leaving time, as dictated by the MVT, for a flock of n parasitoids parasitizing a host patch of quality q. The dictum of the combined LMC-MVT theory is that, for all n,

$$\int_0^{t^\star_{n,q}} \mu(t) f'(n,q,t)\,\mathrm{d}t = r^\star(n) f(n,q,t^\star_{n,q})\,.$$

It follows that necessarily

$$\int_0^{t^\star_{N,q}} \mu(t) f'(N,q,t)\,\mathrm{d}t = r^\star(N) f(N,q,t^\star_{N,q})\,.$$

We may choose $\mu(t) = r^\star(N) =: \mu_N$ for all $t \in [0, t^\star_{N,q}]$. Also

$$\int_0^{t^\star_{N-1,q}} \mu(t) f'(N-1,q,t)\,\mathrm{d}t = r^\star(N-1) f(N-1,q,t^\star_{N-1,q})\,.$$

Taking the first choice into account, this yields

$$\int_{t^\star_{N,q}}^{t^\star_{N-1,q}} \mu(s) f'(N-1,q,t)\,\mathrm{d}s = \\ r^\star(N-1) f(N-1,q,t^\star_{N-1,q}) - r^\star(N) f(N-1,q,t^\star_{N,q})\,.$$

Again, we may choose $\mu(t) = \mu_{N-1}$ constant for $t \in [t^\star_{N,q}, t^\star_{N-1,q}]$ with

$$\mu_{N-1}\Big[f(N-1,q,t^\star_{N-1,q}) - f(N-1,q,t^\star_{N,q})\Big] = \\ r^\star(N-1) f(N-1,q,t^\star_{N-1,q}) - r^\star(N) f(N-1,q,t^\star_{N,q})\,.$$

More generally, we can compute recursively $\forall t \in [t^\star_{k+1,q}, t^\star_{k,q}]$, $\mu(t) = \mu_k$ given by

$$\begin{aligned} \mu_k\left[f(k,q,t^\star_{k,q}) - f(k,q,t^\star_{k+1,q})\right] &= r^\star(k) f(k,q,t^\star_{k,q}) \\ &\quad - \sum_{\ell=k+1}^{N} \mu_\ell \left[f(k,q,t^\star_{\ell,q}) - f(k,q,t^\star_{\ell+1,q})\right], \end{aligned}$$

with the convention that $f(k,q,t^\star_{N+1,q}) = 0$.

While this defines a time behaviour which does not require that the females be “aware of” the number of competing females on the patch, it is still dependant on their “knowing” the patch quality. To better understand what this implies, it is necessay to take a particular model for f.

3.2 Pure scramble competition

We particularize here our investigation to the theoretical model of scramble competition. We mean a model where the only competition between females is through the sharing, and exhausting, of the same resource, with no further efficiency loss due to fight. We use the model of [HBNW07].

3.2.1 The theoretical model

We summarize here the theoretical model of foraging that we use. The foraging rate of any female is assumed to be a function of the *density* ρ of healthy hosts on the patch:

$$\dot{c} = \varphi(\rho) = \frac{\rho}{\sigma + h\rho} \,.$$

(σ is a “search” time, or inverse of the “attack rate”, and h the “handling” time.) The depletion equation is

$$q\dot{\rho} = -n\dot{c} = -n\frac{\rho}{\sigma + h\rho} \,,$$

while the leaving time is given by $\dot{c} = \gamma^\star$, a fixed parameter depending on the environment. Let thus $\varphi(\rho^\star) = \gamma^\star$.

As a consequence, the foraging function $f(n,q,t)$ can be expressed in terms of a single function $\xi(\cdot)$ defined as the solution of the differential equation $\dot{\xi} = -\varphi(\xi)$, $\xi(0) = 1$, which can also be charcterized as an inverse function:

$$s = h(1 - \xi(s)) - \sigma \ln \xi(s) \,.$$

The foraging function is then

$$f(n,q,t) = q\left[1 - \xi\left(\frac{n}{q}t\right)\right] \,,$$

the optimal leaving time $t^\star_{n,q} = (q/n)\tau^\star$, with $\xi(\tau^\star) = \rho^\star$, definig $\tau^\star$ as a parameter depending on σ, h and $\gamma^\star$ only.[1] As a consequence, $f(n,q,t^\star_{n,q}) = q(1-\rho^\star)$.

3.2.2 The egg-laying strategy

Let us use the above model in our egg-laying strategy. An elementary calculation yields

$$\mu_k\left[\xi\left(\frac{k}{k+1}\tau^\star\right) - \rho^\star\right] = r^\star(k)(1-\rho^\star) - \sum_{\ell=k+1}^{N} \mu_\ell\left[\xi\left(\frac{k}{\ell+1}\tau^\star\right) - \xi\left(\frac{k}{\ell}\tau^\star\right)\right] .$$

Both q and n seem to have disappeared from the definition of this behaviour. This is not quite so. As a matter of fact, recall that the dictum is

$$\forall t \in \left[\frac{q}{k+1}\tau^\star, \frac{q}{k}\tau^\star\right] \,, \quad \mu(t) = \mu_k$$

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[1] $\rho^\star = \sigma\gamma^\star/(1-h\gamma^\star)$, and $\tau^\star = h(1-\rho^\star) - \sigma\ln\rho^\star$.

This definition involves q. If we think that the female parasitiods sense the *foraging rate*, which is the customary hypothesis to have a proximal behaviour explaining the MVT, we may replace the above prescription by

$$\text{as long as } \dot{c} \in \left[\varphi \circ \xi \left(\frac{n}{k}\right), \varphi \circ \xi \left(\frac{n}{k+1}\right)\right] , \quad \mu = \mu_k \, .$$

However, the whole purpose was to eliminate n, a failure so far ! Remind that this is

Work no longer in progress

References

[Cha76] Eric Charnov. Optimal foraging: the marginal value theorem. *Theoretical Population Biology*, 9:129–136, 1976.

[Ham67] William Donald Hamilton. Extraordinary sex ratios. *Science*, 156:477–488, 1967.

[HBNW07] Frédéric Hamelin, Pierre Bernhard, Philippe Nain, and Éric Wajnberg. Foraging under competition: evolutionarily stable patch-leaving strategies with random arrival times. 1. scramble competition. In Thomas Vincent, editor, *Advances in Dynamic Game Theory*, volume 9 of *Annals of the International Society of Dynamic Games*, pages 327–348. Birkhaüser, 2007.

[Nag94] Cornelis J. Nagelkerke. Simultaneous optimization of egg distribution and sex allocation in patch-structured populations. *The American Naturalist*, 144:262–284, 1994.

[NvBS96] J. Nagelkerke, Cornelis, Minus van Baalaen, and W. Sabelis, Maurice. When should a female avoid adding eggs to the clutch of another female ? *Evolutionary Ecology*, 10:475–497, 1996.

[Waa86] J.K. Waage. Family planning in parasitoids: adaptive patterns of progeny and sex allocation. In J. K. Waage and D. Greathead, editors, *Insect parasitoids*, pages 63–95. Academic Press, London, 1986.

[Waj94] Éric Wajnberg. Intra-population genetic variation in *trichogramma*. In E. Wajnberg and S. A. Hassan, editors, *Biological Control with Egg Parasitoids*, pages 245–271. CAB International, 1994.

[WL84] J. K. Waage and J. A. Lane. The reproductive strategy of a parasitic wasp ii. sex allocation and and local mate competition in *trichogramma evanescens*. *Journal of Animal Ecology*, 53:417–426, 1984.

[WN84] J. K. Waage and S. M. Ng. The reproductive strategy of a parasitic wasp i. optimal progeny and sex allocation in *trichogramma evanescens*. *Journal of Animal Ecology*, 53:401–415, 1984.

[Qo940BC] Solomon. Ecclesiastes, chapter 1, verse 9. In *the Bible*, circa 940 BC