PATCH-EFFICIENT PARASITOIDS, CHAOS AND NATURAL SELECTION

J. C. ALLEN
Department of Entomology and Nematology
University of Florida
Gainesville, Florida 32611-0143 U.S.A.

ABSTRACT

The nonlinear dynamics view of population interactions emphasizes three critical points: 1) instability does not imply extinction, 2) very complicated behavior is possible from very simple systems, and 3) if density-dependence occurs as lagging nonlinear feedback, then it is the primary cause of instability and chaos and does not stabilize populations in contrast to the traditional view.

Discrete time (“Nicholsonian”) host-parasitoid models are used to illustrate that a patch-efficient parasitoid is destabilizing when searching a patchy host distribution. When some very crude genetics are added in terms of parameter phenotypes (patchy and random hosts and patchy and random parasitoid search strategies), then there is a much wider variety of dynamic behavior. In general, selection does not seem to work for or against chaotic parameter phenotypes. Instead, it appears to increase the likelihood of chaos (i.e., at lower parameter values) and decrease the likelihood of extinction of chaotic systems if they occur.

RESUMEN

El punto de vista no lineal y dinámico de interacciones de poblaciones hace incapí en tres punto críticos: 1) inestabilidad no implica extinción; 2) un comportamiento muy complicado es posible en sistemas muy simples; y 3) si la densidad dependencia ocurre como un retardo no lineal retroactivo, entonces es la primera causa de inestabilidad y caos, lo que no estabiliza las poblaciones contrariamente al punto de vista tradicional.

Los modelos hospedero-parasitóide de tiempo discreto (“Nicholsoniano”), son utilizados para ilustrar que un parasitóide parche eficiente está es destabilizador cuando este busca la distribución en parches del hospedero. Una amplia variedad de comportamiento dinámico en términos de parámetros fenotípicos (hospederos al azar o en parches y estrategias de búsqueda al azar o en parches) ocurre cuando algunos aspectos de la genética básica son adicionados. En general, la selección parece no trabajar para o en contra de los parámetros de fenotipos caóticos. Por el contrario, parece incrementar la probabilidad de caos (esto es, a bajos valores del parámetro) y decrece la probabilidad de extensión de sistemas caóticos si ellos ocurrieran.

The subtle and clever mechanisms by which insect parasitoids locate their hosts are a continuing source of wonder to biologists (Cade 1975, Walker 1986, Lewis & Tumlinson 1988). Modeling the population dynamic consequences of efficient non-random search behavior by parasitoids (“aggregation to host density”) is the subject of a large and active literature (Hassell & May 1973, 1974, Beddington et al. 1978, May 1978, May & Hassell 1981, Heads & Lawton 1983, Waage 1983, Hogarth & Diamond 1984, Chesson & Murdoch 1986, Walde & Murdoch 1988). Much of this work was probably stimulated by Nicholson’s early comment that his elegant but unstable host-parasitoid model might be stabilized by “the breaking up of the species population into numerous small widely separated groups which wax and wane and then disappear, to be replaced by new groups in previously unoccupied situations” (Nicholson & Bailey 1935).
Many complications and misunderstandings have beset the work on host-parasitoid “stability” from the beginning. First of all stability came to be used in a narrow sense to mean attraction to a fixed point equilibrium. When contrasted with Nicholson’s oscillations of increasing amplitude, one gets the notion that the only biological alternative to an attracting fixed point is extinction (at least locally). Obviously, a more detailed and sophisticated view of dynamic behavior is required for an understanding of ecological systems. A more refined view of dynamic motion has recently arisen from the field of nonlinear dynamics with particular reference to ecology (Schaffer & Kot 1985, 1987, Allen, in press). Even the engineers have been somewhat narrow in their approach to dynamics, and “tutorials” on the dynamic possibilities have been written from the engineering perspective (Parker & Chua 1987), so it is scarcely surprising that ecologists have had a problem. Briefly stated, some of the dynamic possibilities are:

*Attracting point:* a fixed point equilibrium to which the system is attracted.

*Attracting or limit cycle:* an unvarying cycle with constant period and amplitude into which the system is attracted.

*Toroidal flow:* motion on the surface of a torus (i.e., a doughnut) resulting from the interaction of two (or more) cycles (one around the axis the other around the center of the torus). Two possibilities have been recognized in terms of the periods of the cycles:
  1) The ratio of the periods is rational (a whole number ratio). In this case the motion will be truly periodic.
  2) The ratio of the periods is irrational (not a whole number ratio). In this case the motion is said to be *quasiperiodic* or *almost periodic*. A good example is the “wagon wheel effect” in old western movies when the wheels appear to be rotating slowly forward or backward due to the interaction of the film cycle and the wheel cycle.

A much more rigorous technical definition is given by Parker & Chua (1987).

*Chaos:* This can be loosely defined as “none of the above.” It is bounded attracting dynamic behavior that is not an attracting point, not periodic and not quasiperiodic. It is sensitive to initial conditions in that initially close points do not stay close but separate at an exponential rate while staying in the bounded region (the “attractor”).

This short discourse on non-linear behavior is included here to emphasize its importance when considering ecological systems. Even in the most sophisticated mathematical models of host-parasitoid interactions (e.g., Chesson & Murdoch 1986, Murdoch et al. 1987), the principle focus is still on stable vs. unstable behavior with the implication that instability and extinction go hand-in-hand. There is nothing in the nonlinear behaviors defined above which dictates extinction of species having “unstable” dynamics, and even chaos does not *necessarily* imply extinction. It could be argued that what we are talking about here is “mathematical” stability vs. “biological” stability, but since the mathematics is an attempt to describe the biology, the two should be compatible. Instability and even local extinction could be tolerated easily by species with high rates of movement, and this may be the rule rather than the exception in host-parasitoid systems with high rates of attack and reproduction. Thus, nonlinear dynamics, instability and, even chaos at the local population level do not imply extinction of the species (i.e., biological disaster). In fact, natural selection acting on individuals to produce high reproductive and attack rates may actually promote unstable or even chaotic dynamics at the local level. We will investigate this in some models below.

One final word about density-dependence as a “stabilizing” mechanism in ecology: it is difficult to envision density-dependence (i.e., nonlinear density feedback) as an instantaneous process. That is, most such processes (e.g., reproductive feedback, predator numerical responses, disease transmission, etc.) logically involve some sort of associated lag in the process before its feedback effects are felt by the system. But lagging nonlinear feedback along with periodic forcing are the primary causes of instability and chaos in nonlinear systems (Allen, in press). Thus, expecting to find direct density-dependence in field data on real systems seems a bit simplistic considering the complexity
of the situation (see, for example, Schaffer & Kot 1986). In fact, density-dependence may be present, it may go undetected because of the lags involved, and it may be destabilizing the system anyway and even producing chaos at the local level if it is strong enough. It is, therefore, no surprise that one can show such seemingly odd things as inverse density-dependence stabilizing a population (Hassell 1984, Chesson & Murdoch 1986) and that one can easily illustrate systems in which density-dependence is present but nearly impossible to detect (Hassell 1985). Thus, lagging density-dependence could be all around us but simply be very difficult to detect by conventional approaches to field data, and it would probably tend to destabilize populations rather than stabilize them anyway. When the full range of nonlinear behaviors is considered, the traditional search for stabilizing density dependence seems much too narrow in its approach. Better perhaps would be to search for any sort of attracting behavior in some space-time window which we find convenient or which seems biologically meaningful.

HOST-PARASITOID MODELS INCORPORATING SPATIAL BEHAVIOR BY THE PARASITOID

In this section some extensions of Nicholson-Bailey discrete generation host-parasitoid models will be considered which attempt to include parasitoid behavior and genetics. Full analysis will be avoided and the emphasis will be on methods and ideas about behavior and/or genetics in these models. The basic general form will be

\[ H_{t+1} = F(H_t, P_t) \]
\[ P_{t+1} = H_t [1 - f(\cdot)] \]

in which \( f(\cdot) = f(H_t, P_t) \) is the fraction of hosts \( (H_t) \) which escapes the attack of the parasitoid \( (P_t) \). \( F \) is the host's reproductive function, which is often assumed constant, but if \( F \) is allowed to express density dependence in the host population, i.e., \( F(H_t) = \exp[r(1-H_t/k)] \) as per Beddington et al. (1975, 1978) then the dynamic behavior covers a wider range of possibilities (including chaos). One simplified version we will consider is

\[ x_{t+1} = x_t \exp[r(1-x_t) - (\gamma y)^{1-m}] \]
\[ y_{t+1} = y_t [1 - \exp(-\gamma y)^{1-m}] \]

(Allen, in press). This relationship incorporates Beddington's host density-dependence and also the notion of parasite mutual interference (competition) \( m \) after Hassell & Varley (1969). The equilibrium point for host and parasite densities will be stable (i.e., "attracting" for nearby densities) if the largest root \( (\lambda) \) of the characteristic equation of the system is less than one in absolute value, i.e., \( |\lambda|_m < 1 \) (Allen, in press). In Figure 1, \( |\lambda|_m \) is plotted over the \( (r, m) \) plane for different \( \gamma \) values. For unstable parameter combinations \( (|\lambda|_m > 1) \), the computer set \( |\lambda|_m = 1 \), producing the effect of an unstable "plateau" for these values of \( (r, m, \gamma) \) and a stable "valley" for stable regions. Chaotic dynamics appear in parts of the unstable regions of this model (Allen, in press). Since \( r \) and \( Y \) are the host reproductive rate and parasite attack rate, we have the result that high \( r \) and/or \( \gamma \) are destabilizing and may cause high amplitude chaotic oscillations and local extinctions (particularly for high \( \gamma \)). For \( r = 2, m = 0 \) and \( \gamma = 7 \) (a fairly efficient parasite) the model is chaotic (Fig. 2), and it appears that such an intense interaction might cause local extinction.

The phenomenon of chaos is interesting enough in its own right, but in biological population systems it poses some very fundamental and interesting questions. For example, could natural selection acting on individuals produce behavioral phenotypes having chaotic population parameters? Would these populations then have a high likelihood of local extinction?
Fig. 1. Stability surface for the host-parasitoid model eqns. (2). The model is stable for $|\lambda|_m < 1$ (the “valley” in the figure) and unstable when $|\lambda|_m > 1$ (the “plateau” in the figure). The unstable plateau to the left of the stable valley increases in size with increasing parasite efficiency ($\gamma$). Chaotic and quasiperiodic dynamics occur for parameter values in this region.

In an attempt to answer such questions consider a modification of eqns. (2) (with $m = 0$ for simplicity) with $x', y'$ representing the $t+1$ values of $x$, and $y$, (again to simplify the writing). This gives

$$x' = xe^{(1-x)-\gamma y}$$
$$y' = x(1-e^{-\gamma y})$$

where the fraction of the host found per parasite ($\gamma$) is given by

$$\gamma = ak$$

where $a$ is the fraction of the area searched/parasitoid (Nicholson’s “area of discovery”) and $k$ is the environmental carrying capacity of the host (Oster 1976; Allen, in press). As illustrated in Figures 1 and 2 the model tends to be destabilized by increasing parasitoid efficiency ($\gamma$).
Host Parasitoid Model

Fig. 2. Dynamics of the host-parasitoid model eqs. (4) for $r = 2$, $\gamma = 7$ (or eqs. (2) with $m = 0$). Chaotic oscillations occur in both host and parasitoid (a,b) and a chaotic or strange attractor is present in the parasitoid-host plane (c). With $\gamma = 7$ this parasitoid is so effective that it would probably cause local extinction.

Suppose now that the host changes its spatial distribution from random to patches of area $\sigma$ (Fig. 3). If the parasitoid's original search covered an area $s (s > \sigma)$ the fraction of this area containing hosts is now $N \sigma/s$ where $N$ is the number of patches in area $s$. 
Host Patches within
Parasitoid Search Window

Fractional Host Area = Nσ/s
(N = Patch Density)

Fig. 3. A parasitoid searching an area of size s containing N host patches each of area σ. The fraction of the host found by a randomly searching parasite is Nσ/s.

If the parasitoid searches this new host distribution at random, its effective area of discovery is reduced to a(Nσ/s), and the host carrying capacity in s becomes k(Nσ/s). The new γ for the patchy host distribution is then given by

\[ γ_s = γ(Nσ/s)^2 \]  

(6)

Thus, if a parasitoid searches a large area s at random for hosts in small patches of area σ, γ_s will be greatly reduced over a parasitoid that confines its search to the patches. This suggests that a parasitoid which was strongly attracted to host patches would increase and tend to destabilize an otherwise stable interaction. If we let s, the area actually searched by the parasitoid, be λNσ (λ ≤ 1), then we can think of 1/λ as a parasitoid patch-concentrating factor and eq. (6) becomes

\[ γ_s = γε^2 \]  

(7)

where ε = 1/λ can be interpreted as parasitoid patch efficiency (0 < ε ≤ 1). The model, eqs. (4), can now be written as

\[ x' = xe^{r(1-x)} - γε^2 y \]
\[ y' = x(1-e^{-nx}) \]  

(8)
where, as we might suspect, the model is destabilized by parasites with high patch efficiency (Fig. 4). This is not meant to imply that parasite aggregation to host density (Chesson & Murdoch 1986, Walde & Murdoch 1988) will always be destabilizing. More complex models with more explicit patch-level dynamics might have different behavior. It does seem intuitive, however, that a parasitoid which is highly effective in locating its host will tend to eliminate the host from local areas and hence to have unstable local dynamics (regardless of how the parasitoid finds its host).

**Effect of Parasitoid Patch Efficiency**

Fig. 4. Effect of parasitoid patch-finding efficiency (ε) when searching for a host which is distributed in patches (eqs. (8), r = 2, γ = 7). The dynamics are chaotic for ε = 1.0 (a,b), quasiperiodic cycles occur when ε = 0.75 (c,d). Attracting fixed points occur when ε = 0.5 (e) and ε = 0.4 (f). Graphs (b) and (d) plot points only for a very long time (10,000 points). For ε<0.3, the parasitoid dies out and the host has persistent cycles of its own.
Surely the evolutionary battle between hosts and parasitoids must play an important role in their dynamical interaction. Several authors have considered this battle in both predator-prey type models (Pimentel 1961, Lomnicki 1971, Stewart 1971, Levin 1972) and competition models (León 1974, Lawlor & Maynard-Smith 1975, Rocklin & Oster 1976). Little attention has been given, however, to the interaction between natural selection and chaos, i.e., whether natural selection might favor chaotic parameter phenotypes in some situations.

Using the Nicholsonian framework, eqs. (4), and the previous discussion of a “patch-efficient” parasitoid, we impose a minimum level of genetic complexity: a “patchy” host phenotype and a “random” host phenotype having reproductive rates \( r_1 \) and \( r_2 \) at frequencies \( p \) and \((1-p)\). In addition, we assume a “patchy” parasitoid phenotype and a “random” parasitoid phenotype at frequencies \( u \) and \((1-u)\). The situation is illustrated in Figure 5 where different attack rates (\( \gamma_{11}, \gamma_{12}, \gamma_{21}, \) and \( \gamma_{22} \)) have been assigned to

<table>
<thead>
<tr>
<th>Parasitoid</th>
<th>Patchy Search</th>
<th>Random Search</th>
</tr>
</thead>
<tbody>
<tr>
<td>Frequency</td>
<td>( u )</td>
<td>( 1 - u )</td>
</tr>
<tr>
<td>Patchy</td>
<td>( r_1, \gamma_{11} )</td>
<td>( r_1, \gamma_{12} )</td>
</tr>
<tr>
<td>Random</td>
<td>( r_2, \gamma_{21} )</td>
<td>( r_2, \gamma_{22} )</td>
</tr>
</tbody>
</table>

Fig. 5. Two parasitoid phenotypes: patchy search and random search present at frequencies \( u \) and \((1-u)\) attacking two host phenotypes: patchy distribution and random distribution present at frequencies \( p \) and \((1-p)\). We assume that the patchy parasitoid is more efficient against the patchy host and conversely, so that \( \gamma_{11} > \gamma_{21} \) and \( \gamma_{22} > \gamma_{12} \). The patchy host and random host have reproductive rates \( r_1 \) and \( r_2 \), respectively.
the four possible types of encounters. We tacitly assume that the "patchy" parasitoid phenotype is a patch efficient parasitoid as described in the previous section and, conversely, the random parasitoid phenotype is more efficient at finding randomly distributed hosts, i.e., in the convention of Figure 5, that \( \gamma_{11} > \gamma_{21} \) and \( \gamma_{22} > \gamma_{12} \). Using the phenotype frequencies we an now write the system from eqs. (4) as a weighted sum of mutually exclusive proportions:

\[
\begin{align*}
    x' &= px\pi^p(1-x) [ue^{-\gamma_{11}\phi} + (1-u)e^{\gamma_{21}\phi}] + (1-p)x\pi^p(1-x) [ue^{-\gamma_{22}\phi} + (1-u)e^{-\gamma_{12}\phi}] \\
    y' &= y[p(1-e^{-\gamma_{22}\phi}) + p(1-u)(1-e^{-\gamma_{12}\phi}) + (1-p)(1-e^{-\gamma_{11}\phi}) + (1-p)(1-e^{-\gamma_{21}\phi})] \\
    p' &= px\pi^p(1-x) [ue^{-\gamma_{11}\phi} + (1-u)e^{\gamma_{21}\phi}]x' \\
    u' &= u[p(1-e^{-\gamma_{22}\phi}) + (1-p)(1-e^{-\gamma_{12}\phi})]y'
\end{align*}
\]

(9)

where \( x \) and \( y \) are the host and parasitoid, and \( p \) and \( u \) are the proportions of patchy hosts and patch efficient parasitoids, respectively. Notice that \( p' \) and \( u' \) are simply the fraction of the total reproductive output which is patchy host and patchy parasitoid phenotype, respectively. Thus, eqs. (9) represent an extension of eqs. (4) which crudely incorporate the dynamics of natural selection on phenotypes.

While eqs. (9) still omit many relevant details, and have the limitation of a discrete time framework, their behavior is remarkably complicated and varied. One can find virtually any kind of dynamical behavior simply by varying the 6 parameters and initial conditions. While it is tempting to illustrate them all, there is neither time nor room here, and only two examples are illustrated in Figures 6 and 7. Both densities and phenotype frequencies apparently can be chaotic (Fig. 6), and initial conditions alone can determine the kind of behavior which is observed (Fig. 7). In this regard, Figure 7 illustrates what appears to be chaos (but may be very complicated quasicycles) (Fig. 7a) in host-parasitoid densities and a beautiful attractor for phenotype frequencies (Fig. 7b), which may be chaotic or a very complex quasicycle (it is difficult to say which without further analysis). When initial conditions are changed, one finds much simpler quasicycles (Fig. 7c-d). This is not to say that other attracting behaviors do not exist elsewhere in the initial condition space. I do not know.

Quasicycles in the phase plane (host vs. parasite) have the appearance of loops of string, and during simulation, plotting points only, one sees the points progressing around on this loop until (if one plots many of them) they fill the loop completely (Fig. 7c-d). Phase plane portraits of chaotic attractors, using points only, tend to show a discontinuous structure (Fig. 6b-c).

**DISCUSSION AND CONCLUSIONS**

From these results we cannot be sure if selection for chaotic parameter phenotypes is likely to occur in host-parasitoid systems. It does seem fairly certain in this conceptual framework that increasing parasitoid patch-finding efficiency destabilizes the interaction, making chaos and local patch extinction more likely (Fig. 4), and in a general way this makes intuitive sense. When genetics are added to the system in the form of two simple parameter phenotypes for each species, dynamic behavior is more complex, with extinction seeming somewhat less likely even for chaotic oscillations (Figs. 6-7).

Local patch extinction (whether the result of chaotic oscillations or whatever) does not imply species extinction. One has, in addition to intrapatch dynamics, an interpatch dynamics, so the question of whether patch chaotic oscillations would cause patch extinction is a moot point. The question really is: could one have chaotic interpatch dynamics with frequent patch extinction without intrapatch (species) extinction. In such a system we would see local chaos, but the species would endure.

As it was constructed here, the genetic model did not always go to fixation of the highest reproductive rate host and the most efficient parasitoid (although this can hap-
Host–Parasitoid "Genetic" Model

Fig. 6. Host-parasitoid "genetic" model, eqs. (9), \( r_1 = 1, r_2 = 2, \gamma_{11} = 5, \gamma_{12} = 2, \gamma_{21} = 3, \gamma_{22} = 6 \). Initial conditions are: \( x = 0.1, y = 0.1, p = 0.5, u = 0.5 \). Apparent chaotic oscillations occur for both density and phenotype frequency. On the left (a,c) are short time period graphs after allowing 500 time points for transient behavior to decay. On the right (b,d) are 10,000 points plotted in the phase plane.

pen in some cases). Instead, the system exhibits a great variety of dynamical behaviors depending upon the parameters and initial conditions. It is interesting in this regard that the system in Figure 6 simply has an attracting 6-point cycle for the highest reproductive and attack rates (\( r = 2, \gamma = 6 \)), but it is chaotic in density and phenotype frequency once both phenotypes are present (even though the added phenotypes have lower reproductive and attack rates).

A similar kind of phenomenon occurs in the example of Figure 7. For the highest reproductive and attack rates there (\( r = 1.5, \gamma = 7 \)), a simple quasicycle is observed which goes so close to zero as to suggest local extinction. When both phenotypes are present, neither densities nor phenotype frequencies go to extinction, and simple quasicycles coexist with apparently chaotic behavior determined by initial conditions alone.

From both of these examples it appears that the addition of simple genetic selection to the interaction has not indicated selection for or against chaotic parameter phenotypes. Instead, the addition of genetics seems to have increased the likelihood of chaos (i.e., at lower parameter values) and decreased the likelihood of extinction of chaotic systems if they occur.
Sensitivity to Initial Conditions

Fig. 7. Different qualitative behaviors obtained from the host-parasitoid genetic model, eqs. (9), by shifting the initial conditions. (In all graphs 10,000 points are plotted in the phase plane.) Parameters are the same for all graphs: \( r_1 = 1, r_2 = 1.5, \gamma_{11} = 5, \gamma_{12} = 2, \gamma_{21} = 3, \gamma_{22} = 7 \). The initial conditions (i.c.) for (a,b) are \( x = 0.1, y = 0.1, p = 0.5, u = 0.5 \). For (c,d) the i.c. are \( x = 1, y = 0.05, p = 0.1, u = 0.9 \). Thus, one can have behavior (a,b) or behavior (c,d) simply by an initial condition change.

ACKNOWLEDGMENTS

I am indebted to Sandra J. Walde and J. H. Frank for helpful reviews. I also thank Barbara Hollien for her patient typing and Susan Marynowski for help in preparing the figures. This is Florida Agricultural Experiment Station Journal Series No. 9685.

REFERENCES CITED


THE PYCOMERINI (COLEOPTERA: COLYDIIDAE)
OF THE WEST INDIES

MICHAEL A. IVIE
Department of Entomology
Montana State University
Bozeman, MT 59717 USA

AND

STANISLAW A. ŚLIPIŃSKI
Institute of Zoology
Polish Academy of Sciences
ul. Wilcza 64
00-679 Warsaw, POLAND

ABSTRACT

Eight species of Pycnomerus Erichson are recorded from the West Indies. A lectotype is designated for Penthelia longior Grouvelle, which is placed in synonymy with Penthelia inffima Grouvelle as Pycnomerus inffimus NEW SYNONYMY, NEW COMBINATION. A lectotype is designated and the type locality restricted to Puerto Rico for Penthelia corpulenta Reitter, with Penthelia aequicollis Reitter placed as a junior synonym, under the name Pycnomerus corpulentus NEW SYNONYMY, NEW COMBINATION. A lectotype is designated for Pycnomerus biimpressus Reitter. The following species are described as NEW SPECIES: P. annae (Jamaica), P. darlingtoni (Jamaica), P. hottae (Haiti), P. uniformis (Guadeloupe), and P. valentinei (Hispaniola). A key and illustrations are provided for the identification of adults of West Indian Pycnomerus species.

RESUMEN

Se registran ocho especies de Pycnomerus Erichson en las Indias Occidentales. Se designa el lectotipo de Penthelia longior Grouvelle, cual especie está reconocida como sinónimo de Penthelia inffima Grouvelle NUEVO SINÓNIMO, y está listada como Pycnomerus inffimus (Grouvelle) NUEVO COMBINACIÓN. Se designa el lectotipo de Penthelia corpulenta Reitter, y la localidad del tipo está limitada a Puerto Rico. Penthelia aequicollis Reitter se reconoce como sinónimo de esta especie y aparece como Pycnomerus corpulentus (Reitter) NUEVO SINÓNIMO, NUEVA COMBINACIÓN. Se designa el lectotipo de Pycnomerus biimpressus Reitter. Se describen cinco Nuevas Especies: P. annae (Jamaica), P. darlingtoni (Jamaica), P. hottae (Haiti), P. uniformis (Guadalup), y P. valentinei (La Española). Hay ilustraciones y una tabla diamóntica para facilitar la identificación de los adultos de las especies de Pycnomerus de las Indias Occidentales.