



# Pest science in Pasteur's Quadrant

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## Abstract

More than 25 years ago, Donald Stokes argued that we must move beyond the false dichotomy of basic or applied research and suggested that when considering a program of scientific research it is important to ask whether (i) the work is motivated by use and (ii) if there is a search for fundamental understanding. Giving yes/no answers to these questions allows us to characterize research more fully, replacing the “or” of “basic or applied” by a richer understanding of the process of science. Stokes proposed that research that was motivated by a consideration of use and sought fundamental understanding be called research in Pasteur's Quadrant. One advantage of such work is that the search for fundamental understanding means that the problem-solving tools are more likely to be transferrable. After reviewing Stokes's formulation of research, I illustrate it with examples from the control of tephritid flies and the use of insect parasitoids for biological control. Thinking about one's work within Stokes's framework has many advantages for individual scientists, including guidance for journal selection, how to organize and conclude papers and seminars, and the “elevator speech.” Furthermore, since research in Pasteur's Quadrant has the characteristic of simultaneously increasing our understanding of how the world works and improving applications, it will more likely benefit the community of pest scientists.

**Keywords** Pasteur's quadrant · Agricultural pest control · Mediterranean fruit fly · Apple maggot fly · Rose hips fly · Insect parasitoids

## Key Message

When work is motivated by consideration of use and seeks fundamental understanding, it has the greatest possibility of providing transferrable tools that can be used in specific situations in pest science and of simultaneously adding to our fundamental understanding and improving applications

## Introduction

Louis Pasteur discovered that the growth of microbes was responsible for spoiling milk

And he invented a process of heating milk to kill the microbes and prevent it from spoiling.  
 Louis Pasteur discovered that a disease caused by microbes was killing silkworms  
 And he developed a process to eliminate the microbes, protect the silkworms and ultimately save the French silk business.  
 Louis Pasteur discovered that he could artificially weaken disease-causing microbes  
 And he created some of the earliest vaccines, exposing people to the weakened microbe to foster immunity to the stronger form. (Levin 2017)

Levin continued “It was the ‘ands’ that stuck with me. Some of Pasteur's peers were solely on a quest for fundamental understanding. Others were less interested in knowledge for knowledge's sake—but rather sought to practically apply existing knowledge. Pasteur was different. He pushed the frontiers of knowledge, but did so because he saw a real-world need. Pasteur sought to uncover nature's secrets—and

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use this wisdom to improve the human condition... We conservation scientists must follow in Pasteur's footsteps—steadfast in our learning and resolute in its application. By conducting such use-inspired research, our scientists have the best hope of developing novel, practical, applicable and scalable solutions to the wicked problems (*sensu* Rittel and Webber 1973) our ecosystems face.”

Although Levin was writing about conservation science, the ideas apply equally well to pest science, which is as broad as nature itself. Because of that breadth, framing the questions (and answers) in pest science can be a daunting task. In this essay, I introduce and explain Donald Stokes's notion of Pasteur's Quadrant (Stokes 1997) and show how it provides a superb conceptual framework for pest science.

In his book *Pasteur's Quadrant* Stokes (1997) argued that a single axis between basic and applied science is the wrong way to think about things. Rather, one must focus attention in a plane. One axis of assessment of work is whether it is motivated by a consideration of use and the other is whether there is a quest for fundamental understanding. The plane can then be divided into the four quadrants (Fig. 1): (1) No consideration of use and quest for fundamental understanding; (2) Consideration of use and a quest for fundamental understanding; (3) Consideration of use and no quest for fundamental understanding; and (4) No consideration of use and no quest for fundamental understanding.

Stokes called the quadrant “not motivated by consideration of use and search for fundamental understanding” Bohr's Quadrant (although we are now clearly aware of the

uses of Bohr's work understanding the atom), the one “motivated by consideration of use and no search for fundamental understanding” Edison's Quadrant and the quadrant “motivated by consideration of use and search for fundamental understanding” Pasteur's Quadrant. For obvious reason, the fourth quadrant remains unnamed.

Stokes emphasized these quadrants doing so replace the “or” in the linear “basic or applied” description of science by “and.” He wrote “Pasteur wanted to understand *and to control* the microbiological processes he discovered. Keynes wanted to understand *and to improve* the workings of modern economies. The physicists of the Manhattan Project wanted to understand *and to harness* nuclear fission. Langmuir wanted to understand *and to exploit* the surface physics of electronic components. The molecular biologists have wanted to understand *and to alter* the genetic codes in DNA material” (pp. 80).

Pasteur's entire career involved work that was motivated by consideration of use in which he simultaneously sought fundamental understanding (Debr'e 1994). Pasteur himself said “There is no such thing as a special category of science called applied science; there is science and there are its applications, which are related to one another as the fruit is related to the tree that has borne it” (Debr'e 1994).

One advantage of working in Pasteur's Quadrant is that we are most likely to develop transferrable methods when we seek fundamental understanding, so that we can simultaneously advance fundamental understanding and the application of science. Pest science has not yet been framed using the ideas from Stokes, but Rosenheim and Coll (2008) is in the spirit of Stokes's ideas, with pest-centric research roughly corresponding to Edison's quadrant and process-centric research roughly corresponding to Pasteur's quadrant.

		Considerations of use?	
		No	Yes
Quest for fundamental understanding?	Yes	Pure basic research (Bohr)	Use-inspired basic research (Pasteur)
	No		Pure applied research (Edison)

**Fig. 1** Stokes's (1997) vision of science is that in every scientific endeavor we may ask if there consideration of use motivating this work and whether or not there is a quest for fundamental understanding. Niels Bohr provides the canonical example of an individual whose work was not motivated by consideration of use but involved the deep search for fundamental understanding and Thomas Edison one whose work was motivated by consideration of use but did not search for fundamental understanding. Louis Pasteur's work from the time of his PhD onwards was motivated by consideration of use (Debr'e 1994) while he simultaneously sought fundamental understanding

## Framing research in pest science via Pasteur's quadrant

### Situating work in Stokes's quadrants

Our work in pest science can fall into any of the quadrants in Fig. 1. To make these ideas concrete, I use my own work on fruit flies of economic importance and insect parasitoids to illustrate how one's work can fall into each of the named quadrants in Fig. 1 and how that influences the questions we ask and what we do.

When I arrived at UC Davis (UCD) in 1980, the infestation of Mediterranean fruit fly [medfly] *Ceratitis capitata* (Wiedemann) in northern California was a matter of scientific and public concern. Medfly is a pest throughout the world, attacking a wide range of fruit and causing considerable economic damage. Thus, there is great concern about it

becoming established in a new region. Carey (1991) gives a summary of the situation a decade after the 1980s infestation and Papadopoulos et al. (2013) an overview of tropical fruit fly (medfly and other species) invasions in California from a longer viewpoint. Debate on the nature of these invasions continues to this day (e.g., Carey et al 2017).

Very shortly after my arrival at UCD, James Carey, Richard Plant and I started working on a question concerning the medfly eradication program that sits squarely in Edison's Quadrant. That work led me to another question in Pasteur's Quadrant, and the development and application of state-dependent life-history theory implemented by Stochastic Dynamic Programming (SDP; explained below) to host choice and movement in insects, and ultimately to a question in Bohr's Quadrant concerning host feeding by insect parasitoids. I describe each of these in turn and explain at the end of each subsection why I put the research into that quadrant.

### An investigation in Edison's quadrant: spatial organization of traps to delimit pest infestations

Here, I draw heavily on Mangel et al (1984). By the early 1980s, there was a protocol for placing medfly traps during the Northern California eradication campaign. One goal of trapping during an eradication campaign is to provide

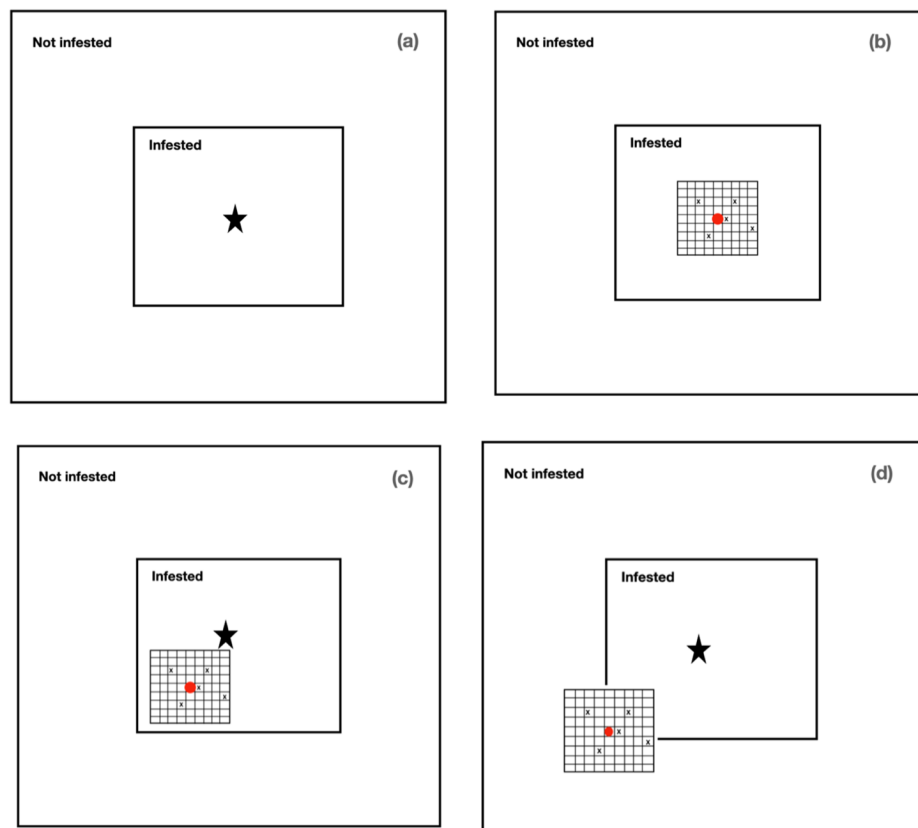
information about the extent of the infestation. If pests are found at a point in space, then one knows that the infestation extends to that point. If pests are not found, however, one does not know that pests are absent since they could be present but not trapped.

In brief, the protocol in 1980 was this. Most potential infestation locations had approximately ten traps per square mile; these traps were inspected weekly. When a medfly was found in a trap, the density of traps was increased to fifty per square mile in a 9 mile  $\times$  9 mile region surrounding the point of detection. All additional traps were inspected daily, and within 48 h of detection the 9  $\times$  9 mile region was sprayed with malathion.

To begin thinking about trapping protocols, envision (Fig. 2) a large region in which a subregion is infested with a pest. For simplicity, we assume that the epicenter (the point of highest pest density) occurs in the center of the infested region; this is denoted by a star. When a positive trapping event occurs, the trapped fly could be near the epicenter of the infestation, removed from the epicenter but in a way so that the additional traps all fall within the infested region, or on the boundary of the infestation so that many of the additional traps fall outside of the infested region.

Figure 2 helps make clear the fundamental intuition that trapping a fly does not mean that location of the trapping

**Fig. 2** Visualization of the medfly trapping protocol in the 1980s infestation in Northern California. **a** We envision a large region in which a subregion is infested with a pest. These are drawn as symmetrical squares. For simplicity, we assume that the epicenter (the point of highest pest density) occurs in the center of the infested region; this is denoted by a star with other cells containing pests denoted by **x**. The entire region has traps that are inspected regularly. Now imagine that a positive trapping event, denoted by the red circle, occurs. The trapped fly could be **b** at the epicenter of the infestation, **c** in the infested region in a manner in which all of the additional traps fall in the infested region or **d** in the infested region but on its boundary so that many of the additional traps fall outside of the infested region



event is the “epicenter” of the infestation. This leads us to ask: what is the probability that any spatial point  $(x, y)$  in the region is the epicenter of the infestation, given that a fly was trapped at spatial point  $(i, j)$ ? This is essentially a search problem, which can be answered by application of Bayes’ theorem of conditional probability (Mangel 1981). We (Mangel et al 1984) explored different forms for the spatial distribution of the infestation before trapping information was collected, used empirical information about the efficacy of individual traps and explored two relationships between the number of traps placed and the probability of trapping a fly given that it is present (trap efficiency, which may show diminishing returns as the number of traps increases).

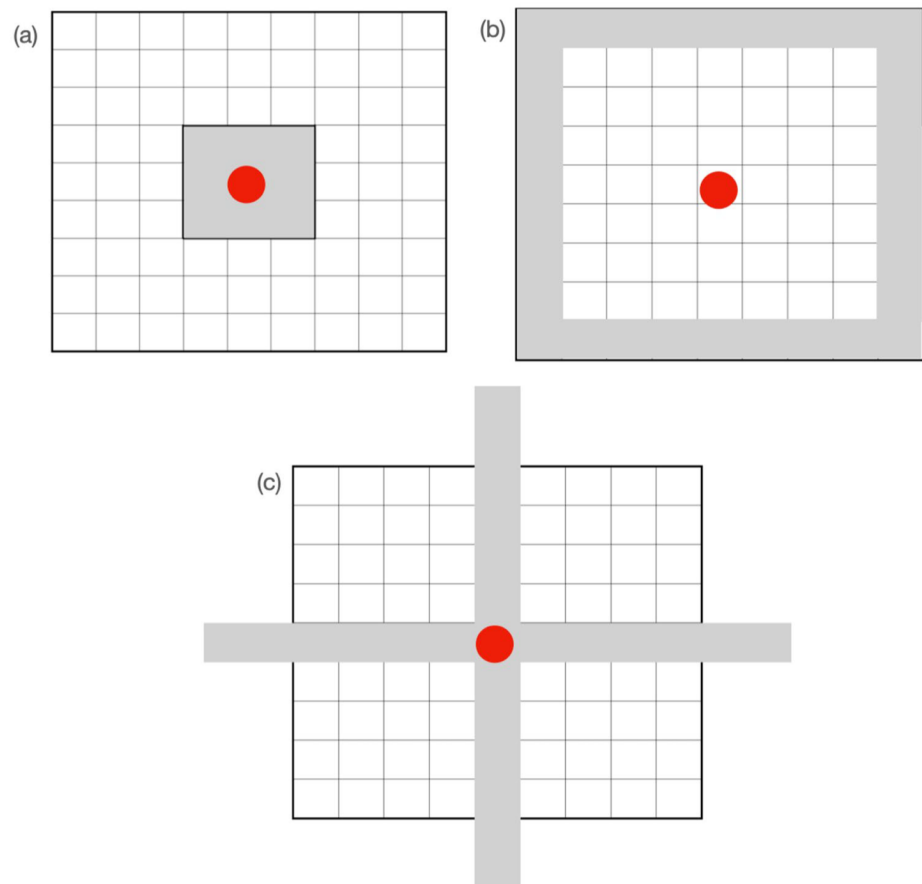
Intuition suggests that in the early stages of determining the boundaries of an infestation (delimiting of an infestation), when the infestation may already be quite widespread, one may want to put the extra traps around a perimeter some distance from the presumed epicenter of the infestation. That is, the operational suggestion is that trappers should start from the perimeter and work in toward the putative center. On the other hand, when delimiting satellite infestations that are less likely to be widespread, the placement of the extra traps near the presumed epicenter may be most effective.

When pests are found in the traps that are furthest from the original trapping event, one knows that the infestation extends to that point. However, when pests are not found it does not necessarily mean that pests are absent from the outer ring. It is possible that they are present but were not trapped. We used a series of analytical models and Bayesian reasoning to compute the probability that pests were present but not trapped. A key parameter in those results was the characterization of the spatial pattern of pests, which is driven by pest behavior but is also generally unknown.

To explore and quantify this intuition, we used Monte Carlo simulation to assess the ability of alternative spatial distributions of the additional traps to provide better information than the protocol then used, which implicitly assumes that the motivating detection is the center of the infestation. 2. Three choices are: 1) the protocol at that time (50 traps per cell in the region surrounding the motivating trapping event; Fig. 3a) and two alternatives: traps placed uniformly on the perimeter of the region (Fig. 3b), and traps placed as a cross, extending past the region of interest (Fig. 3c), since we actually never know the boundaries of that region.

In the simulation, we tracked a variety variables including the average and coefficient of variation of the number of flies

**Fig. 3** Three possible spatial organizations for additional traps in a  $9 \times 9$  mile square with a pest trapped at its center: **a** the extra traps placed surrounding the trapped pest (the protocol at the time we did our work), **b** the extra traps placed on the perimeter of the  $9 \times 9$  mile square around the original trapping event and **c** traps placed in a cross that goes past the boundary of the  $9 \times 9$  mile square surrounding the original trapping event



captured during the simulated time period, the average and coefficient of variation of detected extent of the infestation. Among other things, we discovered that placing extra traps in a cross shape centered at the point of first detection is an efficient pattern worthy of serious consideration in future outbreaks.

I put this research into Edison's quadrant because our focus was the best way to use the additional traps to delimit the infestation. We did not seek fundamental biological understanding about the trapping process, such as how the fly's behavior responds to the plume of chemicals from the trap (cf. Mangel 1986). Had we continued this research, with a greater focus on fundamental understanding, as in the more recent work of Caton et al (2021) and Fang et al (2022), it could traverse from Edison's quadrant to Pasteur's quadrant.

Although this is a problem in Edison's Quadrant, the methods that we used—both analytical and simulation—were not trivial. That is, a problem in Edison's quadrant can be very difficult to solve and one needs to bring to the problem whatever tools will do the job; sometimes the simpler tools will do the job (Hammersley 1974) but other times not. Always, we must keep our eyes on the prize.

#### **An investigation in Pasteur's quadrant: host choice, individual movement and the spread of pest infestations**

I was sufficiently excited about bringing ideas from search theory to agricultural pest control, that I sought and found funding for a research workshop on operations and systems analysis in fruit fly control (Mangel et al. 1986). I left the workshop convinced that understanding the spread of pest infestations required a program of theoretical and empirical research concerning oviposition behavior and movement in insects.

Concomitantly, Colin Clark and I were developing the ideas that lead to state-dependent life history and behavioral theory implemented by Stochastic Dynamic Programming (SDP; reviewed in Mangel and Clark (1988), Clark and Mangel (2000), Mangel (2015)). The fundamental understandings about insect oviposition behavior are described in Chapter 4 (coincidentally) of both Mangel and Clark (1988) and Clark and Mangel (2000). This work provides relatively complete answers to questions such as “how many eggs do we predict an insect to lay in a host with given volume [or other appropriate characteristics] depending on time available for search and oviposition, the number of eggs the female currently harbors, and the rate of mortality she experiences?”, “under what circumstances do we predict a female will lay an egg in a host that already contains eggs laid by a conspecific (or possibly even her)?”, or “for parasitoids that host feed, when do we predict a female will host feed rather than lay an egg in a host she encounters?” We will return to the last question in the next section.

For the empirical side of the investigation, I established a collaboration with Professor Bernard Roitberg (Simon Fraser University, Canada). We conducted a long-term study of the host choice and the spatial patterning of egg laying in another tephritid fly *Rhagoletis basiola*, which attacks the wild roses. *R. basiola* is not an economic pest, but it is a congener of the apple maggot fly *R.pomonella*. By using the rose hips fly, we were able to conduct field experiments that would not be easily done with an actual pest but with confidence that what we learn about the behavior and control of this fly should be transferable to pest control (one of the key reasons to work in Pasteur's Quadrant).

The life history of the rose hips fly in brief: Adults are free ranging and live for about three weeks. In southwestern British Columbia, where we worked, they emerge in late July just as the fruit are ripening. The fruit are clustered, with up to seven fruit in a single cluster, but usually between two and five fruit in a cluster. Clusters are spatially aggregated. A female typically lays about ten eggs per day, usually one egg per fruit that she attacks. After laying an egg [parasitizing a host (Price, 1989)], she drags her ovipositor across the fruit, marking it with a pheromone (Prokopy 1972). After landing on a fruit, a female walks around it a number of times; tarsal receptors respond to marking pheromone and in this way she can determine if the fruit has been previously parasitized. On occasion, females will superparasitize and lay an egg in a previously parasitized fruit, even though only one offspring emerges from the host.

In the wild, the main sources of mortality of adult flies are strong rain storms, birds and spiders. The main source of mortality of the eggs, which are laid under the skin of the fruit, is the parasitoid *Halticoptera rosae*, which uses *R. basiola* marking pheromone and fruit wound chemicals to find eggs (Roitberg and Lalonde 1991).

Our field work was motivated by the observation that *Rhagoletis spp.* often do not attack apparently perfectly healthy, unparasitized fruit. For example, the apple maggot fly in a semi-natural setting exploited only between 5 and 30% of the uninfested hosts (Roitberg et al. 1982).

In 1992, we observed a similar phenomenon with flies attacking clusters of wild roses. For example, although all clusters of seven fruit had at least one egg in them, most (55%) had only one fruit of the seven attacked and 90% of the clusters had three or fewer fruit attacked. When flies are not ovipositing in every fruit in a cluster, they are moving to new clusters for additional ovipositions, which clearly has important effects on the determination of damage and on the spread of the infestation. In 1992, we understood why flies might accept a previously parasitized host (Mangel 1987; Roitberg and Mangel 1988), but it remained enigmatic that flies did not lay eggs in perfectly fine hosts. To say they were “spreading the risk” describes the phenomenon, but does not provide a functional explanation for their behavior.

To develop such a functional explanation, we must be able to describe the spatial characteristics of the environment encountered by a fly in a manner that allows those characteristics to interact with the behavior and reproductive success of the fly. Here I found an important gap in the way that spatial information was characterized, and an opportunity to increase fundamental understanding with the control of tephritid flies not far from my mind.

It is common in spatial statistics to use the semivariogram to summarize the degree of spatial structure in patchily distributed resources (Wikle et al 2019). For example in the case of rose hip flies, the semivariogram captures how clusters of rose hips differ (e.g., in the number of hips per cluster) according to how far apart they are. While this information is valuable for surveys, it is less valuable to an individual rose hips fly that has the behavioral choice of ovipositing or not in the current cluster. This is the gap that needed to be filled.

Intuition tells us that from the fly's perspective there is something fundamentally different between a spatial point that has a cluster of rose hips and one that does not. For example, if the plants are not resource limited in any way, then when a fly is at a cluster of rose hips, it is likely that there are other clusters close by. If the plants are resource limited, then there may be resource halos in which the probability of another cluster being close to the current cluster is lower than the probability of another cluster being further from the current cluster.

To capture this idea, I developed the notion of functions that characterize the structure of the environment via the probability  $p(r|1)$  that a spatial location  $r$  units away from the current location has a cluster of fruit, given that the current location has a cluster of fruit (indicated by the 1 following the vertical bar in  $p(r|1)$ ) and the probability  $p(r|0)$  that a spatial location  $r$  units away from the current location has a cluster of fruit, given that the current location is devoid of fruit (indicated by the 0 following the vertical bar in  $p(r|0)$ ). Clearly, as  $r$  increases, each of these functions should approach the average availability of fruit in the environment (Mangel and Adler 1994; Fig. 4a, b here).

In Fig. 4c and d, I show structure functions for wild rose bushes at six different locations in British Columbia (slightly modified from Roitberg and Mangel (1997)). We combined this field information on spatial structure with field information on mortality while moving between clusters, laboratory information on mortality while ovipositing and on the relationship between clutch laid and emerging offspring from a rose hip to compute the expected lifetime reproductive success (LRS, fitness) of life-history strategies characterized by movement from a location that had fruit, movement from one that did not have fruit, and the number of eggs laid in a host.

Given the shape of the structure functions in Fig. 4c, it was not surprising that the optimal (i.e., maximizing LRS) movement distance from a location that had a cluster was always one spatial unit. However, the optimal movement distance from a location that did not have fruit varied from 1 spatial unit to 11 spatial units.

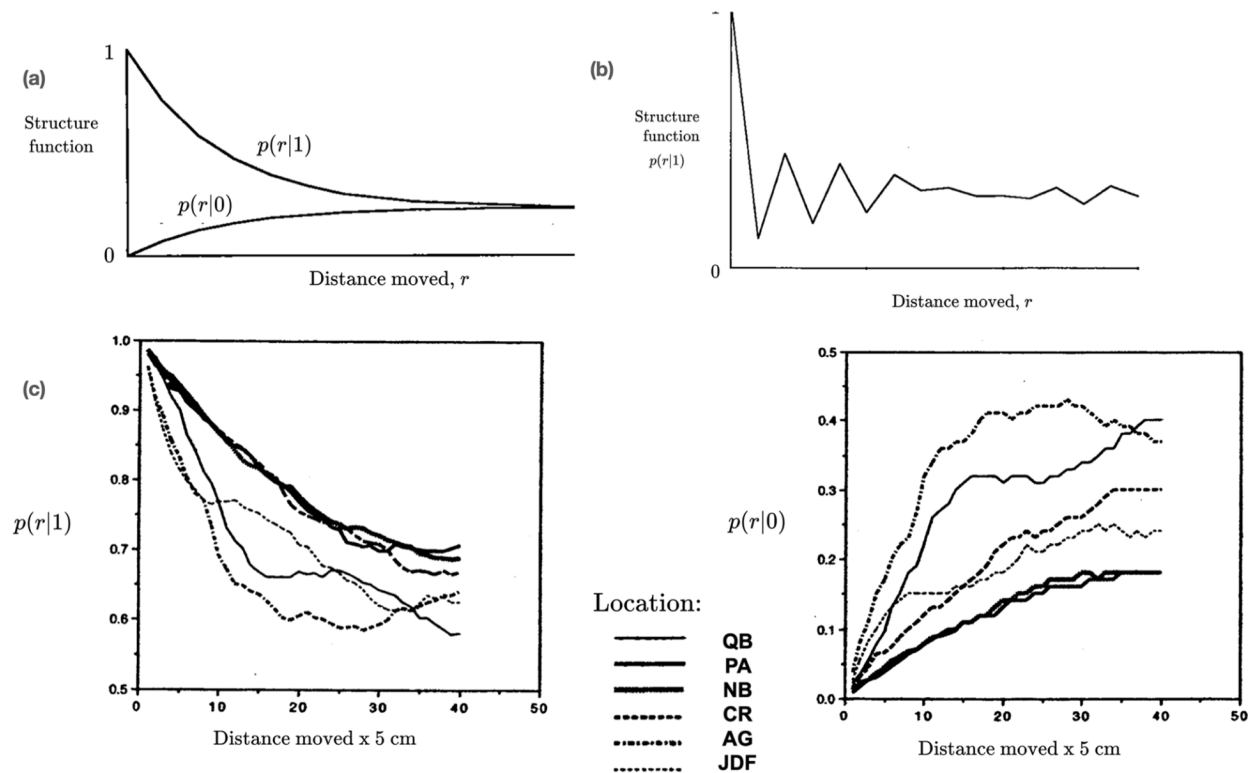
By computing expected lifetime fitness, we were able to address the question of how individual behavior may mitigate different spatial distributions of resources. We discovered that it is possible to group the sites according different criteria. For example, when we asked which sites were similar according to structure, based on  $p(r|1)$  they were organized as {CR, NB, PA}, {JDF}, {AG, QB}; when we grouped according to  $p(r|0)$ , they were organized as {NB, PA}, {CR, JDF}, {QB}, {AB}. When we asked which sites were similar according to expected reproductive success, we grouped them as {AG, QB}, {NB, PA}, {CR} and {JDF}. This kind of information is valuable when considering conservation efforts that require determining which sites are exchangeable and which are more unique. The use of these ideas in conservation only came up after we had started working on them, motivated by the spread of pest infestations, which is another benefit of working in Pasteur's Quadrant.

I put this work into Pasteur's quadrant because we were motivated by the control of pest infestations (and subsequently by conservation applications) and sought fundamental understanding (using functional descriptions of behavior) about why the flies were moving in space and time. One of the advantages of working in Pasteur's Quadrant is that we learn to see commonalities in systems that are very different on the surface. For example, I applied the notion of structure functions to understand how vessels fishing for southern ocean krill moved (Mangel 1994).

### An investigation in Bohr's quadrant: combining matrix methods in stochastic dynamic programming

To illustrate an example in Bohr's Quadrant, I turn to insect parasitoids and an insight developed by Jody Reimer in the course of her PhD work (Reimer et al 2019). Many parasitoid wasps can either consume a host (host feed) or oviposit in a host when one is encountered [e.g., Jervis and Kidd (2008), Jervis and Ferns (2011)]. Which they do will determine the effectiveness of the wasp as a biological control agent (Heimpel and Mills 2017).

Intuition suggests that when a parasitoid has many resources, she will be more likely to oviposit in a host, thus obtaining an immediate increment in lifetime reproduction with a concomitant reduction in her resources. On the other hand, when she has fewer resources intuition suggests that she will be more likely to feed on the host, thus foregoing immediate reproduction but obtaining resources that can be used in future reproductive opportunities. As with the



**Fig. 4** The structure function characterizes spatial information in a way that is relevant to the behavior of an insect. Panels **a** and **b** show conceptual examples of the probability  $p(r|1)$  that a spatial location  $r$  units away from the current location has a cluster of fruit, given that the current location has a cluster of fruit (indicated by the 1 following the vertical bar in  $p(r|1)$ ) and the probability  $p(r|0)$  that a spatial location  $r$  units away from the current location has a cluster of fruit, given that the current location is devoid of fruit (indicated by the 0 following the vertical bar in  $p(r|0)$ ). Note that panel **b** has a resource halo around locations of fruit. See Mangel and Adler (1994) for further details. Panels **c** and **d** show the structure functions of wild rose

bushes measured in southwestern British Columbia (BC), Canada (Roitberg and Mangel 1997). The location codes are AG: Aggasiz, about 100 km east of Vancouver; CR: Crofton, about 50 km south of Nanaimo, Vancouver Island; JDF: Juan de Fuca, about 100 km east of Victoria, Vancouver Island; NB: Nanoose Bay, about 45 km north of Nanaimo, Vancouver Island; PA: Parksville, about 50 km north of Nanaimo, Vancouver Island; QB: Qualicum Beach, about 55 km north of Nanaimo, Vancouver Island. Panels **a** and **b** modified from Mangel and Adler (1994); panels **c** and **d** modified from Roitberg and Mangel (1997)

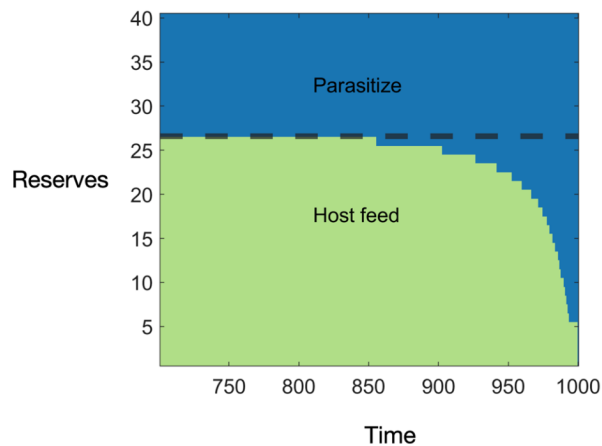
problems in Edison's Quadrant and Pasteur's Quadrant, a quantitative approach allows us to make the intuition more predictive.

In the simplest state-dependent life-history modeling implemented by Stochastic Dynamic Programming for host feeding or oviposition, there is a single state variable, reserves, with a particular value denoted by  $r$ . Without losing any generality, we can assume that when reserves fall to 0 the parasitoid dies and that when the parasitoid is killed (e.g., by a storm or spider) reserves jump to 0 from whatever value it had before the mortality event. And once a  $r=0$ , reserves stay at that value forever.

In the simplest case, the dynamics of the reserves can be described as follows: i) it costs one unit of reserves to live a unit of time, ii) if a host is encountered and used for oviposition an additional  $p$  units of reserves are spent on laying an egg in the host, and iii) if a host is encountered and fed upon,

the parasitoid gains  $g$  units of reserves. Thus, if at time  $t$  the reserves are  $r$ , at  $t+1$  they are 0 [if she dies],  $r-1$  [if she does not encounter a host or encounters a host and rejects it for either feeding or oviposition],  $r-1-p$  [if she encounters a host and oviposits in it], or  $r-1+g$  [if she encounters a host and feeds on it]. We can collect these changes together in a matrix that describes the change in reserves of a parasitoid from one time period to the next.

Specifying the resource dynamics, the rate of mortality and the increment in expected lifetime reproductive success from oviposition are sufficient to construct a SDP model that predicts, as a function of state and time, whether a parasitoid is predicted to feed on or oviposit in host (Mangel and Clark 1988; Chan and Godfray 1993; Clark and Mangel 2000 (pp 102–103); Mangel (2015); Reimer et al 2019). The results of the model can be summarized in the state-time plane as a boundary between host feeding and oviposition (Fig. 5).



**Fig. 5** The solution of a state-dependent model for host feeding behavior of parasitoid wasps foraging in predicts as a function of physiological reserves and time whether a wasp is predicted to feed on or oviposit in a host upon encountering it. Far from the time horizon, the boundary is stationary and depends only upon state. By applying matrix methods to policy iteration, Reimer et al (2019) determined the stationary boundary between host feeding and parasitizing, shown here as the dotted line

using the standard method of backward iteration in time and looping over all reserve states for each time step (Mangel and Clark 1988; Clark and Mangel 2000; Mangel 2015). Once the optimal behaviors (oviposit in a host or feed on it) are computed, we can use forward Monte Carlo simulation to create observations of parasitoid behavior.

There is another approach for computing the optimal behavior, called policy iteration (McNamara 1991; Puterman 1994). In this context, a policy is considered as a set of rules that describe behavior over the course of the entire time period of interest. For example, a time independent (stationary) policy might be “host feed if resources are less than a particular threshold value and oviposit otherwise.” A policy might be time and state dependent such as “host feed if resources are less than a particular threshold and time is far away from the end of the season; otherwise oviposit.” Since reserves are always bounded by a maximum value, although there may be many policies their number is limited. Using the matrix of transitions, Markov chain methods allow us to predict the probability distribution of the parasitoids’ state conditioned on the policy (a simple example is given in Mangel and Clark (1988), pp 77–79).

Reimer et al (2019, Sects. 2.4–2.8) show how to reformulate backward iteration of SDP models into matrix form, so that one is maximizing over all policies at once. When the SDP model is written in matrix form, we can employ the long-standing and well-developed matrix methods in population ecology (Caswell 2001) to determine the optimal stationary policy. In addition, reformulating with matrix notation allows relatively easy implementation of Markov

chain analysis to give an exact distribution for the realized states of an individual, rather than Monte Carlo simulations that only give an approximate distribution.

The analytical matrix methods provide the same results as backward iteration far from the time horizon (Fig. 5), and insights into the properties of nearly optimal strategies, which we may also expect to observe in nature. Furthermore, the matrix methods also provide insight into other aspects of SDP models. One property of matrix population models is that as time increases, the solution of a matrix model is determined by the largest (for growing populations) or smallest (for decaying populations) eigenvalue of the matrix. But for times close to the time horizon, more than one eigenvalue of the relevant matrix may characterize the population’s transient behavior. The analogy with matrix behavioral models is that when one is close to the time horizon, behaviors may oscillate as a function of state and time. Understanding those behaviors is very difficult with the standard method of backward iteration, but is relatively easy with the matrix approach.

I put this work in Bohr’s quadrant because our focus was understanding how to link SDP methods and matrix methods, rather than planning to use the linked methods in applications for biological control. In fact, the original motivation for this research was to understand SDP prediction of oscillating behavior for the patch choice problem from Mangel and Clark (1988). Here, the matrix methods show that when one considers times close time horizon, behavior is determined by more than one of the eigenvalues of the transition matrix (Reimer et al 2019, Supplementary material).

### Why spend the time situating your work in Stokes’s quadrants

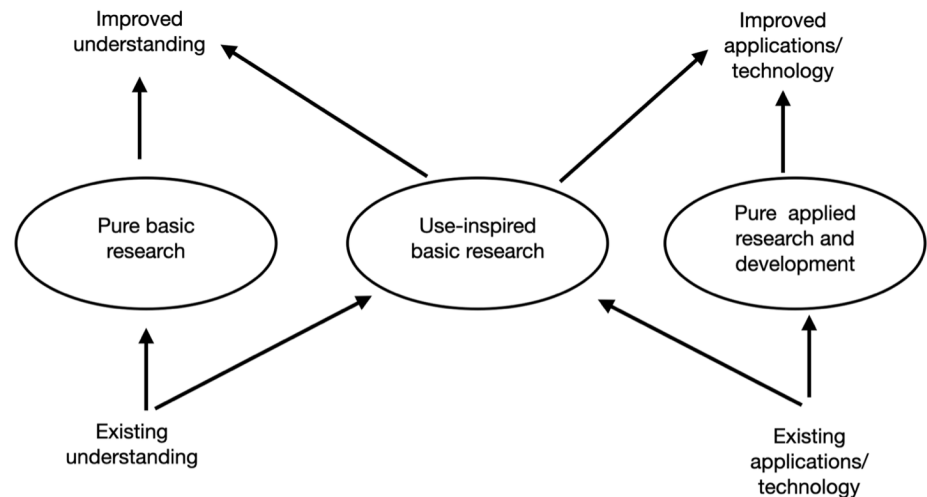
There are advantages to individual researchers for thinking about in which quadrant one’s work falls. These include (i) how to structure papers and seminars, (ii) journal selection and (iii) the “elevator speech.”

When giving department seminars, I find it helpful to introduce the three quadrants and then, depending upon the department, situate the seminar in the relevant quadrant. For example, in a biology department that is knowingly hostile to “applied work,” one might slant the seminar toward Pasteur’s quadrant, in order to emphasize the transferrable knowledge rather than the details of the particular study.

Even though journals may not state in their guideline “we seek papers in Bohr’s/Edison’s/Pasteur’s quadrant,” a quick perusal of a journal will give a sense of which kinds of papers predominate. Thus, if one has developed transferrable methods and ideas by working on a specific species in a specific location and a journal explicitly states that such papers are returned, the way to at least get reviewed is to phrase the work as belonging in Pasteur’s quadrant. At other times, a



**Fig. 6** Stokes (1997) argued that use-inspired research in Pasteur's Quadrant has the greatest capability of leading to both improved understanding and new technology. Modified from Fig. 3–7 in Stokes (1997)



detailed and beautiful study of host selection may simply belong in Bohr's quadrant and one should think of a journal that appreciates such work (not every study has to have immediate use). And there are plenty of situations during pest outbreaks in which work belongs in Edison's quadrant.

Next imagine that on a work trip you are staying in a hotel that has a venue for events on the roof and one day after coming back from work you get into an elevator and meet Bill Gates who asks what you are doing in town. How will you frame the answer to his question?

There are also advantages for the community of pest scientists if work is situated in Pasteur's quadrant (Fig. 6). In particular, Stokes argues that use-inspired basic research has the greatest possibility for simultaneously leading to improved understanding and improved applications. This is a good goal for all of us to seek.

## Future directions and conclusions

It is time for us to put aside the dichotomy of "basic vs applied" research and focus on motivations for the question investigated and the development of transferrable tools via a focus on motivation by an important applied problem and a search for fundamental understanding.

## Author contributions

I am the sole author.

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## Declarations

**Competing interests** The authors declare that they have no competing interests.

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