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Motivation, Learning, and Motivated Learning

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Introduction

As many of the papers in this volume illustrate, the behavior of an organism can be influenced by its own physiological state, by the state of the environment, and by the information that the organism has about the state of the environment. In this chapter, I develop a functional (i.e., evolutionary) approach that can be used to both separate and integrate physiology and environmental information, since each is connected with changes of behavior as a result of experience. The approach is based on dynamic, state-variable modeling (Mangel and Clark, 1988) which explicitly couples physiology and ecology within the framework of a Darwinian measure of fitness and thus responds to Kamil's (1983) call to integrate the "optimization approach" to behavior with other methods of ethology and psychology. Functional interpretations of learning require an assessment of the fitness, measured in terms of expected reproduction, of suites of behaviors. The technique used to determine fitness is called stochastic dynamic programming. Ward (1987) gives a simple example of stochastic dynamic programming for habitat acceptance; this example is in fact a special case of the methods developed by Mangel and Clark (1986).

Definitions

I modify Dudai's (1989, p. 6) definition: *Learning* is "an experience-dependent generation of enduring internal representations *of the external environment*, and/or experience-dependent lasting modification in such representations." In the language of neural networks (Edelman, 1987; Putters and Vonk, 1990) an "enduring internal representation" is a description of the external world based on connections between different neuronal groups and rules for modifying those connections. Learning rep-

resents changes in the pattern of connections or the rules for modifying those connections (e.g., Mangel, 1990a; Putters and Vonk, 1990). External cues and experience lead to modification of the pattern of connections and the rules for modifying those connections. With this definition, an organism cannot learn about its own internal state and learning consists of gathering information about the external environment and using that information to change the description of the environment. For example, if we want to study how oviposition behavior depends upon the rate of encounters with hosts, egg complement and age should be held constant as encounter rates are varied. By holding egg complement constant, we are able to understand how different encounter rates lead to different behaviors at a constant physiological state.

Motivation is a measure of physiological state directly related to the behavior of interest. Changes in motivation, via experience, can lead to changes in behavior, but this is not learning. For example, egg complement will increase over time if hosts are not encountered, and this can lead to a change in behavior (usually acceptance of an inferior host for oviposition). The objective in the host encounter study would be to separate changes in behavior due to increased egg complement (motivation) from changes in behavior due to changed descriptions of the world (learning) as encounter rates with hosts are varied.

The definition of learning that I adopt is narrower than "changes of behavior with experience." Alex Kacelnik (personal communication) has suggested the following analogy (modified for Central California): If I drive a car equipped with automatic transmission from Davis (elevation 19 m) to Lake Tahoe (elevation approximately 2,000 m), the car will change gears as the mountains are traversed. Although these changes of gear are determined by the "experience" of the automobile, they do not represent learning: gear changes are engineered responses to the state of the transmission.

The next two sections contain examples of learning and motivation separately, within the context of a functional determination of the value of information. In the third section, I show how the two can be combined.

Learning: Parasitoids and Patches of *Drosophila*

In this section, I model learning by a drosophilid parasitoid which is time, rather than egg, limited (e.g., van Alphen and Visser, 1990; Janssen, 1989) (see Table 6.1 for an explanation of parameters and their interpretations.) The assumption that the parasitoid is time limited means that the physiological variables (egg complement, nutritional status) can be ignored. In addition, I assume that patches of hosts consist of discrete clumps of rotting fruit which contain larvae of hosts and that the patches are hard to

Table 6.1. Parameters and their interpretations: parasitoids and patches of *Drosophila*

Parameter	Interpretation
λ	Encounter rate of a parasitoid, once it is in a patch of hosts
α, ν	Parameters that describe the probability density of values of λ ; in particular, the mean value of λ is $\frac{\nu}{\alpha}$ and the coefficient of variation is $\frac{1}{\sqrt{\nu}}$
α_0, ν_0	Initial values of the parameters, before a patch is visited; these correspond to “evolutionary information” concerning the distribution of possible values of λ
$f_0(\lambda)$	Prior probability density of λ , before a sampling is done
$\Gamma(\nu)$	Gamma function (for integers $\Gamma(\nu) = (\nu - 1)!$)
$f_p(\lambda K, S)$	Posterior probability density of λ , given that K hosts were encountered in search time S
$F(\nu, \alpha, t)$	Expected (averaged over random encounters with hosts) accumulated ovipositions between t and T , given that the current values of the parameters describing the probability density of λ are ν and α
ρ	Probability that the parasitoid encounters a patch of hosts in a single period of search
μ	Probability that the parasitoid is killed during a single period
V_{leave}	Fitness value of leaving the current patch
N	Random number of hosts encountered in a single period of search, given that the parasitoid is in the patch
V_{stay}	Fitness value of staying in the current patch
m	Memory parameter used to weight past information

find. Since the parasitoid is not egg limited, when such patches are found there are fewer hosts available for oviposition than eggs. Patches of hosts, however, will vary in quality (number of hosts per unit volume, ratio of unparasitized to previously parasitized hosts) both over space and time (i.e., within the context of an individual’s life) and over years (i.e., within the context of evolutionary time).

Here I adapt a model of learning by fishermen (Mangel and Clark, 1983; Mangel, 1990b) to describe learning by such parasitoids. For simplicity, I assume that patches are large enough such that depletion (see Mangel and Clark, 1983) and superparasitism (see Mangel, 1989, 1990b) can be ignored; these can be included in more complex models. In this case, the quality of a patch is determined solely by the encounter rate of hosts within that patch. The objective of the model is to provide a description for learning by the parasitoid as it encounters hosts.

Consider a parasitoid that has already found a patch of hosts. If hosts are randomly distributed in the patch, then we may assume that encounters with hosts in the patch follow a Poisson distribution (random encounters).

Pr {parasitoid encounters k hosts in time t given that the encounter rate is λ }

$$= \frac{e^{-\lambda}(\lambda t)^k}{k!} \quad (1)$$

The encounter rate λ is not known to the parasitoid—it must be learned from experience in the particular patch. There is, however, a priori a probability distribution associated with different values of λ .

This *prior density* of possible values of λ represents an “internal representation” of the world in that the encounter rate in a particular patch is assumed to be randomly drawn from the probability density of λ . Experience (search and encounters with hosts) leads to modifications of this prior density and thus a change of the internal representation. The prior density provides a template for learning; the mechanism of learning still needs to be described.

A commonly used (e.g., DeGroot, 1970; Mangel, 1985) prior density is the gamma density

$$f_0(\lambda) = \frac{e^{-\alpha\lambda}\lambda^{\nu-1}\alpha^\nu}{\Gamma(\nu)} \quad (2)$$

That is, $f_0(\lambda)\Delta\lambda$ is the probability that the actual encounter rate is between λ and $\lambda + \Delta\lambda$. Here $\Gamma(\nu)$ is the gamma function. For integer values, $\Gamma(\nu) = (\nu - 1)!$; otherwise it can be viewed simply as part of the constant that ensures that the integral of $f_0(\lambda)$ over $0 \leq \lambda \leq \infty$ is equal to 1. The gamma density has two parameters, α and ν , that can be interpreted as follows. When λ has the density given by (2), its mean and coefficient of variation (standard deviation divided by the mean) are

$$E\{\lambda\} = \frac{\nu}{\alpha}$$

and

$$CV\{\lambda\} = \frac{1}{\sqrt{\nu}}$$

This form is convenient, because we can specify a mean encounter rate and then adjust the variability of this encounter rate by changing ν .

Combining (1) and (2) shows that

$\Pr \{\text{parasitoid encounters } k \text{ hosts in time } t\}$

$$\begin{aligned}
 &= \int_0^{\infty} \frac{e^{-\lambda t} (\lambda t)^k}{k!} f_0(\lambda) d\lambda \\
 &= \frac{\Gamma(k + \nu)}{\Gamma(\nu)} \left(\frac{t}{\alpha + t} \right)^k \left(\frac{\alpha}{\alpha + t} \right)^\nu
 \end{aligned} \tag{3}$$

This is a negative binomial distribution (Mangel, 1985) and can be put into the form more commonly used by ecologists (Southwood, 1966) in which the mean and overdispersion parameter are specified. One finds that the mean is $m = (\nu/\alpha)t$ and the overdispersion parameter is ν . The mean number of encounters is m and the variance of the number of encounters is $m + (1/\nu)m^2$. Thus, when ν is small, the variance in the encounters will greatly exceed the mean. Parasitoids will experience, once in patches, clumped encounters with hosts: in some patches many encounters will occur and in other patches very few encounters will occur.

Learning is the process of changing the description of the probability associated with different values of λ . We employ the methods of Bayesian updating (DeGroot, 1970). That is, suppose that the parasitoid has been in the patch for S units of time and has encountered K hosts. Learning modifies the prior density by the use of this information and produces a *posterior density of λ*

$$f_p(\lambda | K, S) \Delta\lambda = \Pr \{\text{encounter rate is between } \lambda \text{ and } \lambda + \Delta\lambda, \text{ given that } K \text{ hosts were encountered in } S \text{ units of time}\}$$

Applying Bayes's theorem shows that $f_p(\lambda | K, S)$ is again a gamma density with *updated parameters* $\nu + K$ and $\alpha + S$ (DeGroot, 1970). The Bayesian analysis provides an "updating rule" for the parameters:

$$\nu \rightarrow \nu + K$$

$$\alpha \rightarrow \alpha + S$$

Given the information concerning encounters, the posterior mean and coefficient of variation of λ are $E_p\{\lambda\} = (\nu + K)/(\alpha + S)$ and $CV_p\{\lambda\} = 1/\sqrt{\nu + K}$. These updated parameters represent a change in informational state (estimate of encounter rate distribution) caused by experience (actual encounters with hosts). The prior and posterior densities are "internal representations" which can be modified by experience.

We can compute the selective advantage of learning by relating learning to expected lifetime reproduction of the parasitoid. Assume that at emergence, the prior density of λ (the evolutionary template on which learning occurs) is given by (2) with parameters ν_0 and α_0 and that the maximum reproductive life span of the parasitoid is T . As the parasitoid encounters patches and hosts within patches, the probability distribution of the encounter rate is described by the prior density or the current posterior density. We seek the behaviors that maximize expected lifetime reproduction. In this case, the behavior is particularly simple: the parasitoid can remain in the current patch or leave it and search for another patch. At any time between emergence and T , let

$$F(\nu, \alpha, t) = \text{maximum } E \{ \text{accumulated reproduction from ovipositions between } t \text{ and } T \mid \text{current values of parameters are } \nu \text{ and } \alpha \} \quad (4)$$

The "maximum" in (4) corresponds to a maximum over behavioral decisions (to remain in the current patch or leave) and the " E " denotes expectation over the random distribution of encounters. We can derive an equation for $F(\nu, \alpha, t)$ by considering the consequences of the two behavioral options.

First consider the value of leaving the current patch. If patches are randomly distributed and ρ is the probability that the parasitoid encounters a patch in a single period of search, then the probability that it takes s periods of search to find the next patch is $(1 - \rho)^{s-1}\rho$. If μ is the probability of death in a single period, then the probability that the parasitoid survives these s periods is $(1 - \mu)^s$. If encounter rates in patches are independent of each other, then the expected fitness upon encountering a patch after s units of search will be $F(\nu_0, \alpha_0, t + s)$. That is, since there is no information about the newly encountered patch, we assume that the probability distribution of λ is (2), with the initial parameters ν_0 and α_0 . The fitness value of leaving is thus

$$V_{\text{leave}} = \sum_{s=1}^{\infty} (1 - \rho)^{s-1}\rho(1 - \mu)^s F(\nu_0, \alpha_0, t + s) \quad (5)$$

Since T is the maximum time available for oviposition, if $t + s > T$ in (5), we replace $t + s$ by T .

If the parasitoid stays in the current patch, it may encounter any number of hosts in the next period. This number is a random variable N , with distribution given by (3). For simplicity, assume that superparasitisms are rare. This would occur, for example, if the parasitoid population is low and parasitoids systematically walk along the host patch. In this case, each

encounter with a host increments lifetime fitness by an amount f . The value of staying is composed of two terms. The first is the expected fitness from hosts encountered in period $t + 1$. The second is the expected fitness from hosts encountered after period $t + 1$, taking into account the new information (i.e., that N hosts were encountered in one period of search in the patch). Hence we obtain

$$V_{\text{stay}} = \sum_{N=0}^{\infty} \{Nf + (1 - \mu)F(v + N, \alpha + 1, t + 1)\} \\ \times \left[\frac{\Gamma(N + v)}{\Gamma(v)} \left(\frac{1}{\alpha + 1} \right)^N \left(\frac{\alpha}{\alpha + 1} \right)^v \right] \quad (6)$$

The maximum expected fitness is then determined by comparing the value of leaving the patch and the value of staying in the patch:

$$F(v, \alpha, t) = \max\{V_{\text{leave}}, V_{\text{stay}}\} \quad (7)$$

Eq. (7) is called an equation of "stochastic dynamic programming" (Mangel and Clark, 1988). As seen from the derivation, it is simply a method of bookkeeping, augmented by the assumption that the parasitoid behaves to maximize expected reproduction.¹

The solution of (7) determines values of v and α , as a function of time, for which the parasitoid should stay in the current patch and for which it should leave the current patch. (When $t = T - 1$, the optimal decision is obviously to stay in the patch, regardless of parameter values. This provides a check on the numerical solution).

A number of features emerge from the solution of (7). First (Mangel and Clark, 1983), even in the simplest case of $T = 2$ (so that at most two patches can be encountered), the value of acquiring information and updating parameters as described above can be considerable. For example, when $\rho = 1$ (so a patch is found with certainty in each period), $\mu = 0$ (so that the parasitoid survives each period up to T with certainty), and $\alpha = 0.1$ and $v = 1$ (so that the mean encounter rate is ten hosts per period

¹Computing (5)–(7) is not completely trivial because the sums may involve many terms. This "curse of dimensionality" in dynamic programming is alleviated as better and faster computers allow us to deal with such problems more easily. There are two main difficulties. First, in principle at least, the value of s in (5) and N in (6) may be very large. The way around this difficulty is to choose maximum values of s and N that correspond to most of the cumulative probability (e.g., 99.9%) and restrict s and N to be less-than-or-equal-to those values. The second difficulty is that v can also become very large. Again, a simple solution is to restrict v to be less-than-or-equal-to some maximum value v_{max} in the sense that $N + v$ is never allowed to go above v_{max} .

corresponds to rejection of the host. In this case, one period of time is used, so egg complement is increased by one egg, up to the maximum egg complement. Hence $x' = \min(x_{\max}, x + 1)$.

As (9) is solved for lifetime reproduction, decisions $d_i(x, t)$ are generated. These are to either accept or reject for oviposition a host of type i encountered during period t when egg complement at the start of the period is x . Depending upon the egg complement at the time of acceptance of a host, different clutches will be realized over time and host types. As the difference $T - t$ increases, so that "end of life" effects are less important, the behaviors become independent of time and depend only upon egg complement. From such behaviors, it is possible to predict the results if an insect is presented with a two-type choice experiment (Fig. 6.1).

In such an experiment, an insect is allowed to oviposit. After an interval following the oviposition, she is presented with two hosts and her willingness to oviposit on each host is determined, usually by observing stereotypical preovipositional behavior, but she is not allowed to oviposit (see Singer, 1982, 1983, 1986; Singer et al., unpublished data). This procedure

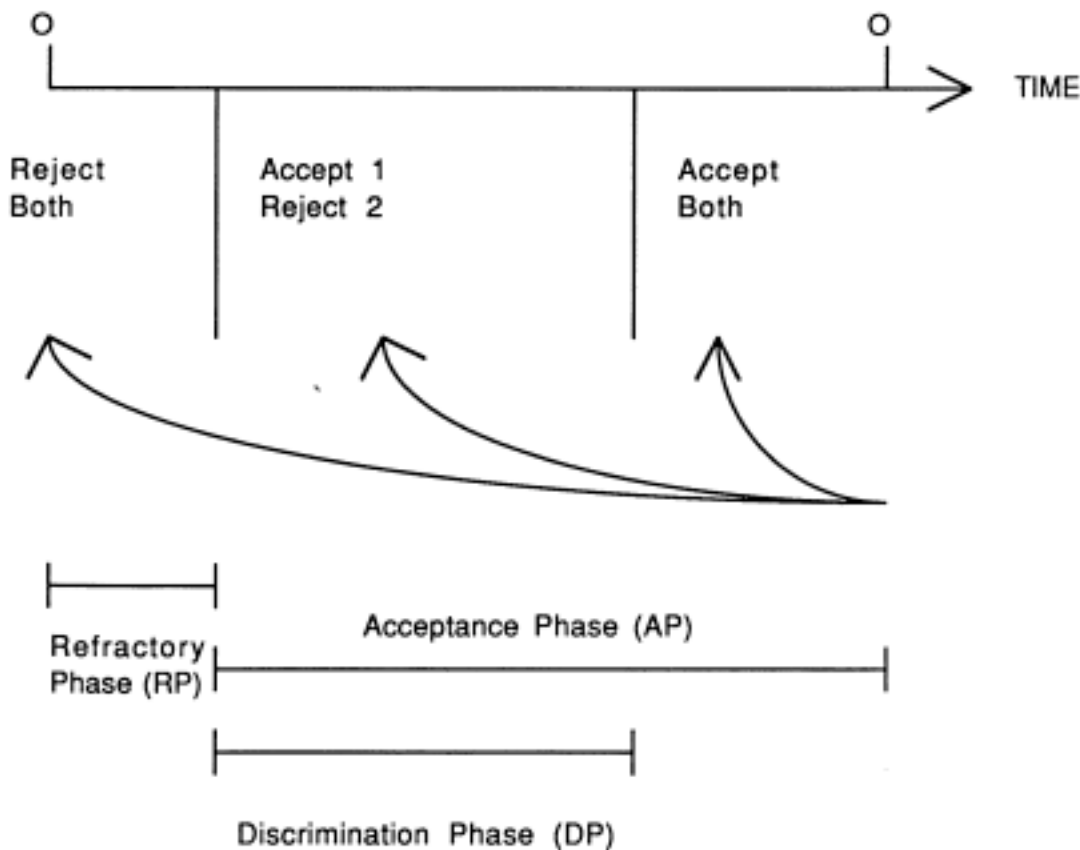


Figure 6.1. Results of the motivational model (9). O denotes an oviposition. See text for further details.

is repeated after another interval. The general prediction, which holds over a wide range of parameter values, for the time course of such an experiment is depicted in Figure 6.1. In the figure, O's denote ovipositions. After the first oviposition, the insect enters a "refractory phase" (RP) in which she rejects hosts, regardless of type. The fixed handling time τ_0 is the source of the refractory period. That is, when τ_0 is very small, we anticipate a small refractory period. Alternatively, when τ_0 is non-negligible, there is a "fixed survival cost" for any oviposition. This causes a delay in oviposition until egg load is such that a sizeable clutch can be laid. For example, laying a single egg requires time $\tau_0 + \tau_1$ and laying ten eggs requires time $\tau_0 + 10\tau_1$. If, for example, $\tau_0 = 10\tau_1$, then the relative risk in oviposition of ten eggs rather than one egg is about twice as great ($20\tau_1$ time units vs. $11\tau_1$ time units), but the relative fitness difference is tenfold if there is no larval density dependence.

As time continues, and egg load increases, there is a point at which the insect will accept type 1 but reject type 2. She is now "motivated" to oviposit and will continue to be so until the next oviposition. For a period defined as the "discrimination phase" (DP), she will be motivated but discriminate between host types 1 and 2 in that she will oviposit in host type 1 but not in host type 2. As time progresses (and no host type 1 is encountered), egg load continues to increase until the insect is both motivated and nonselective. During this "acceptance phase" (AP), the insect will oviposit on the next host presented. After that oviposition, depending upon values of parameters (Table 6.2), the insect may return to any of the three previous behavioral states (RP, DP, or AP). This insect, then exhibits a wide range of behaviors, and these change with experience, although no change of the description of the environment is involved. This is a case in which motivation changes as a result of experience and behavior changes as a result of motivation. However, learning, as defined above, does not occur.

An interesting, possibly counterintuitive, result emerges from this model. The superior host (type 1) will be accepted for oviposition over a wide range of egg complements. The inferior host (type 2) will be accepted for oviposition only for large egg complements, since it is better to oviposit on the inferior host than to simply waste eggs. Because of this, we predict that a range of clutches will be observed on host type 1, but only large clutches will be observed on host type 2. An investigator studying such an insect might reject the "optimality" model because the insect "puts only large clutches into the poor host and this is clearly not optimal." But this is completely consistent with the optimality model. Furthermore, if an investigator simply went to the field and measured clutch sizes as a function of plant quality, he or she could be misled concerning the relationship between preference and host quality or preference and performance. We

Table 6.2. Parameters and their interpretations: behavioral changes induced by egg maturation

Parameter	Interpretation
λ_i	Probability that the insect encounters host type i in a single period of search
f_i	Increment in lifetime reproduction from oviposition of one egg on host type i
$X(t)$	Egg complement at time t
x	Particular value of the egg complement
x_{\max}	Maximum allowed value of the egg complement
$\tau(x)$	Handling time needed to lay a complement of x eggs; it is composed of a fixed time τ_0 and a variable time $\tau_1 x$
$F(x, t, T)$	Maximum expected accumulated reproduction from ovipositions between time t and T , given that the egg complement at time t is $X(t) = x$
μ_{op}	Probability of death during a period in which the insect is ovipositing
μ_s	Probability of death during a period in which the insect is searching

can only understand acceptance of poorer hosts in the context of life history, and not in the context of single host encounters.

We thus see that behavior changes with internal environment (egg complement), which itself changes according to the state of the external environment. This is, however, not learning in that parameters characterizing the external environment are not updated according to experience.

Combining Environmental Information and Physiology: Motivated Learning

The methods of the two previous sections can be combined to deal with motivated learning, i.e., situations in which both an informational state variable, which characterizes the external environment, and a physiological state variable, which characterizes the internal state of the insect, determine behavior. In this case, experience (e.g., host deprivation) changes both the information state (e.g., estimates of encounter rates with hosts) and the physiological state (e.g., egg complement). Mangel (1989) and Mangel and Roitberg (1989) describe two examples in which physiological and informational state variables are combined.

Mangel and Roitberg (1989) considered the so-called superparasitism behavior of the apple maggot *Rhagoletis pomonella*. Female apple maggots

held in field cages usually oviposited in unparasitized fruit and on occasion would oviposit in previously parasitized fruit (i.e., “superparasitize” fruit). Because each fruit in the field cage was individually tagged and individual flies can be observed, the data could be collected according to the encounter history of the fly (the fraction FRAC of previously parasitized hosts in the last five encounters) and the time since the last oviposition (TSLO). Using methods (Iwasa et al., 1984; Mangel, 1987) similar to the ones described in this paper, the plane “TSLO-FRAC” can be divided into two regions. In one region, the next previously parasitized host encountered should be accepted and in the complementary region it should be rejected. When this theory was compared with the empirical results, however, 50% of the observed ovipositions fell into the “wrong” portion of the plane: the flies superparasitized when the theory suggested that they should reject the host. Adding an informational state changes the theoretical predictions. In particular, the TSLO-FRAC is now divided into three regions: one in which the next previously parasitized fruit should be accepted, one in which it should be rejected, and one in which it may be accepted or rejected depending upon the encounter history (information). All but two of the observed acceptances of previously parasitized fruit fell into the “accept” or “maybe” regions (Mangel and Roitberg, 1989: Fig. 4).

Mangel (1989) developed a model for the parasitization of sycamore aphids by *Monoctonus pseudoplatani* Marsh. In this case, the physiological-state variable was egg complement and the informational-state variable was the probability that an encountered aphid would be unparasitized. The patterns of parasitism predicted by the theory compared favorably with the observed patterns of parasitism.

Neither Mangel (1989) nor Mangel and Roitberg (1989) used a Bayesian model of the type described in the current paper. The combination of models of Bayesian updating and physiological variables is an open and fruitful area of research.

Discussion: Can Learning and Motivation be Separated?

In a sense the theory is now ahead of the experimental work, since the task of separating informational and motivational determinants of behavior remains a challenge to empiricists. Progress is being made. For example, Tatar (1991) suggests that informational state (seasonal host quality) interacts with physiological state (egg load) to influence clutch size in oviposition by a butterfly. Rosenheim and Rosen (1991), in an elegant study of the behavior of a parasitoid, show how informational and physiological states may be separated and how the predictions of models such as the ones developed in this paper can be tested. The physiological state variable

(egg complement) was controlled through parasitoid size and ambient temperature. Informational state was controlled by encounter rates, holding egg complement relatively constant.

Roitberg et al. (1992) use photoperiod [the “closeness” of t to T , as in Eq. (4) or (9)] and encounter rates to provide cues about the state of the external environment in situations in which the physiological variable, energy reserves (rather than egg complement), determines survival. Theories similar to the ones developed here are used to predict the time on a patch and number of superparasitisms by a drosophilid parasitoid. The theoretical results are supported by empirical observation.

On the theoretical side, we still need models that effectively describe the “internal representations” in terms of neuronal groups. For example, it is unlikely that animals perform Bayesian updating in the manner described above. On the other hand, it is likely that a neural network which effectively performs the equivalent of Bayesian updating could be constructed and such networks need to be developed. Again, progress is being made (Putters and Vonk, 1990), but there is still much work to be done. The most progress will be made by developing theory and experiments in tandem, so that we will have practicable theories which can provide understanding of experiments on learning and motivation.

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References

- van Alphen, J.J.M., and Visser, M.E., 1990. Superparasitism as an adaptive strategy. *Annu. Rev. Entomol.* **35**:59–79.
- DeGroot, M.H. 1970. *Optimal Statistical Decisions*. McGraw-Hill, New York.
- Dudai, Y. 1989. *The Neurobiology of Memory*. Oxford University Press, Oxford, England.
- Edelman, G. 1987. *Neural Darwinism*. Basic Books, New York.
- Iwasa, Y., Suzuki, Y., and Matsuda, H. 1984. The theory of oviposition strategy of parasitoids. I. Effect of mortality and limited egg number. *Theor. Popul. Biol.* **14**:205–227.
- Janssen, A. 1989. Optimal host selection by *Drosophila* parasitoids in the field. *Funct. Ecol.* **3**:469–479.

- Kacelnik, A., Krebs, J.R., and Ens., B. 1987. Foraging in a changing environment: An experiment with starlings (*Sturnus vulgaris*). In M.L. Commons, A. Kacelnik, and S.J. Shettleworth (ed.), Quantitative Analyses of Behavior, Vol. VI. Foraging. Lawrence Erlbaum Associates, Hillsdale, NJ, pp. 63–87.
- Kamil, A.C. 1983. Optimal foraging theory and the psychology of learning. *Am. Zool.* **23**:291–302.
- Mangel, M. 1985. Search models in fisheries and agriculture. *Lec. Notes Biomath.* **61**:105–138.
- Mangel, M. 1987. Oviposition site selection and clutch size in insects. *J. Math. Biol.* **25**:1–22.
- Mangel, M. 1989. An evolutionary interpretation of the “motivation to oviposit.” *J. Evol. Biol.* **2**:157–172.
- Mangel, M. 1990a. Evolutionary and neural network models of behavior. *J. Math. Biol.* **28**:237–256.
- Mangel, M. 1990b. Dynamic information in uncertain and changing worlds. *J. Theor. Biol.* **146**:317–332.
- Mangel, M., and Clark, C.W. 1983. Uncertainty, search and information in fisheries. *J. Int. Council Explor. Seas* **41**:93–103.
- Mangel, M. and Clark, C.W. 1986. Towards a unified foraging theory. *Ecology* **67**:1127–1138.
- Mangel, M., and Clark, C.W. 1988. *Dynamic Modeling in Behavioral Ecology*. Princeton University Press, Princeton, NJ.
- Mangel, M. and Roitberg, B.D. 1989. Dynamic information and host acceptance by a tephritid fruit fly. *Ecol. Entomol.* **14**:181–189.
- Putters, F., and Vonk, M. 1990. The structure-oriented approach in ethology: Network models and sex-ratio adjustments in parasitic wasps. *Behavior* **114**:148–160.
- Roitberg, B.D., Mangel, M., and Tourigny, G. 1990. Density dependence in fruit flies. *Ecology* **71**:1871–1885.
- Roitberg, B.D., Mangel, M., Lalonde, R.G., Roitberg, C.A., van Alphen, J.J.M., and Vet, L. 1992. Dynamic shifts in patch exploitation by a parasitic wasp. *Behav. Ecol.* **3**:156–165.
- Rosenheim, J.A., and Rosen, D. 1991. Foraging and oviposition decisions in the parasitoid *Aphytis lingnanensis*: distinguishing the influence of egg load and experience. *Anim. Ecol.* **60**:873–893.
- Singer, M.C. 1982. Quantification of host preference by manipulation of oviposition behavior in the butterfly *Euphydryas editha*. *Oecologia* **52**:224–229.
- Singer, M.C. 1983. Determinants of multiple host use by a phytophagous insect population. *Evolution* **37**:389–403.
- Singer, M.C. 1986. The definition and measurement of oviposition preference in plant-feeding insects. In J. Miller and T.A. Miller (eds.), *Insect-Plant Interactions*. Springer-Verlag, New York, pp. 65–94.

- Southwood, T.R.E. 1966. Ecological Methods. Chapman and Hall, London.
- Tatar, M. 1991. Clutch size in the swallowtail butterfly, *Battus philenor*: comparisons of behavior within and among seasonal flights in California. Behav. Ecol. Sociobiol. 28:337–391.
- Ward, S.A. 1987. Optimal habitat selection in time-limited dispersers. Am. Nat. 129:568–579.