

The Dynamics of Specialization and Generalization within Biological Populations

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ABSTRACT. We develop an abstract model to explore specialization and generalization in task performance by individuals within biological populations. Individuals follow simple rules of increasing and decreasing propensities for tasks that could, for example, be based on learning and forgetting. The model does not explore efficiency per se, but makes the prediction that where behavioural specialization occurs in nature, organisms are likely to be reaping sufficient benefits from improved handling efficiency to offset the costs of increased search time. A second prediction is that among specialists, there will be a trade-off between stability and responsiveness. The model reveals potential similarities between a wide range of complex biological systems.

KEYWORDS: Specialists, generalists, simulation model, predation, pollination, switching, task allocation, search image, ants, bumblebees, social insects.

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1. Introduction

One of the greatest contributions of evolutionary biology is recognizing the importance of the uniqueness of the individual (Medawar, 1957). Indeed much of our understanding of evolutionary change through natural selection is associated with genetic biodiversity within populations (Ridley, 1993). However, both nature and nurture contribute to the uniqueness of individuals. Individuals within a population have different genotypes which encounter different environmental influences and such so-called genotype by environment interactions (Falconer, 1981) amplify phenotypic diversity. The most labile and hence arguably the most interesting aspect of phenotypes is behaviour. Here we will focus on behavioural diversity within populations by considering how learning may lead to generalization and specialization and how specialists may switch. These are important considerations over a surprisingly broad range of biological examples.

In ecology, for example, the stability of communities may be greatly influenced by individual predators specializing on one or a subset of many possible prey types (MacArthur, 1955; May, 1973; Pimm and Lawton, 1977). For example, if predators form search images for the more abundant of two (cryptic) prey types they may continue to hunt that prey type disproportionately even when it has become less abundant than the alternative (Begon *et al.*, 1990). Here population dynamics would be linked with the dynamics of individuals learning and forgetting certain search images. Similar reasoning can be applied to the behaviour of pollinators in which members of the same population may specialize in visiting only a subset of accessible flowers (Heinrich, 1979).

The advantage of specialization by individuals within groups is also considered to be of overwhelming importance in many of the major transitions in the evolution of life (Maynard Smith and Szathmary, 1995). One such transition is from single-celled to multicellular organisms; another major evolutionary transition is from solitary organisms to highly social ones. The selective advantage of multicellular organisms over single-celled organisms is probably associated in part with cellular specialization leading to an efficient division of labour (Maynard Smith and Szathmary, 1995). (Implicit in the division of labour is that individuals become more efficient as they specialize (Smith, 1776)). The evolutionary transition from solitary organisms to highly integrated societies (known as eusocial colonies) composed of individual organisms (e.g. ant colonies, termite colonies and certain bees and wasps) is also associated with efficiencies that accrue from a division of labour and task specialization. Social insect colonies have been compared to factories within fortresses (Oster and Wilson, 1978, p. 21-23) and there are many different tasks that workers must perform, from building the

nest and guarding the colony to tending the queen, rearing many different stages of brood, and feeding and grooming one another.

Thus in diverse areas of biology, transitions from generalized behaviour to specialized behaviour are of major evolutionary importance. Clearly, there are fundamental differences, that must not be overlooked, between the systems we have just described. For example, individual predators will specialize on particular types of prey for their own immediate benefit, whereas cells within an organism, or ants within a colony, may specialize for mutual benefit (favouring the selfish genes they have in common). In other words, specialization within organisms or societies occurs because the entities involved belong to a community of mutual interest (Cosmides and Tooby, 1981; see also Bourke and Franks, 1995) and co-operate to favour their self interest indirectly, whereas specialization within ecological populations of distantly related individuals occurs due to direct self interest. Recognizing such fundamental differences should not, however, obscure key similarities in the dynamics of specialization and switching. It is these similarities that we explore here, by considering a model that investigates the dynamics of specialization within populations.

2. The Model

In outline:

- 1 Agents encounter one or more tasks in their environment.
- 2 At each time step each agent may perform one task.
- 3 If it performs a particular task its propensity to perform that task increases.
- 4 If it does not perform a task its propensity for performing the task decreases.

In detail:

Tasks are abstracted as discrete items, one task item being defined as the amount of task that one agent can complete in one unit of time. Hence we have not modelled the effects of changing task efficiency. For simplicity and generality, we have not specified time scales. All the parameters of the model scale with the time step. The reason for this is that time scales for different organisms are likely to differ over several orders of magnitude, and the time period represented by one time step must reflect the behaviour under consideration.

Space is not modelled explicitly; instead, each agent experiences a probability, P , of encountering a task item during each time step. This probability is defined as

$$P = \frac{T}{(T + \alpha)} \quad (2.1)$$

where T is the total number of task items within the simulation, and α is a parameter relating the size of the arena within which the agents and tasks exist to the physical size of a task item and the area searched by an agent within one timestep. This provides a reasonable approximation for the situation where individuals and task items are distributed randomly within an arena of fixed size. At each time step, each agent has a probability P_n of encountering an item of each task, n , such that

$$P_n = \frac{T_n}{(T + \alpha)} \quad (2.2)$$

where T_n is the number of items of task n within the simulation.

At the start of the simulation, each individual has the same propensities for carrying out each specific task. These propensities represent the probability that, on encountering an item of task x , the individual will work on that task item. If an individual's propensity for carrying out task x is defined as π_x , then when the individual encounters an item of task x it has probability π_x of working on that item.

If a task item is worked on by an agent, the task item disappears from the simulation for all future time steps, and the individual's propensity for that task is increased by

$$\Delta\pi_x = \pi_x(1 - \pi_x)\lambda \quad (2.3)$$

Simultaneously, for all tasks n other than x , the individual's propensity decreases by

$$\Delta\pi_n = -(\pi_n(1 - \pi_n)\phi + \pi_n\phi^2) \quad (2.4)$$

Thus if an individual performs a task, it becomes $\Delta\pi_x$ more likely to perform that task should it encounter it in the next time step, and it becomes less likely to perform every other task by $\Delta\pi_n$ where π_n is its previous propensity for that task.

Task choice is determined purely by individual task propensities that are adjusted according to task experience. However, it is essential that a mechanism should exist to prevent task propensities from becoming trapped at zero. For the types of situation we model here, stochastic effects mean that, in time, individuals will always fail to encounter any given task for a long enough period

of time that their propensity for that task reaches zero. Once a propensity has reached zero, the individual will never perform that task and so there will be no potential for its propensity to increase again. Unless individuals can be assured of a constant supply of a task for which they have high propensity, they must become prepared to do tasks which they would at first refuse if faced with a persistent dearth of their ‘preferred’ task(s).

We incorporate such a mechanism into this simulation by allowing individuals’ propensities for all tasks to approach a low but non-zero ‘resting level’, R , on each occasion that a task item is refused. On refusal of a task item, for all tasks n ,

$$\Delta\pi_n = - \left(\frac{(\pi_n - R)(1 - \pi_n)\phi}{1 - R} + \frac{(\pi_n - R)\phi^2}{1 - R} \right) \quad (2.5)$$

if $\pi_n > R$, or

$$\Delta\pi_n = \frac{\pi_n(R - \pi_n)\phi}{R} + \frac{(R - \pi_n)\phi^2}{R} \quad (2.6)$$

if $\pi_n < R$.

In the model, the relationship between propensities and time is sigmoidal, given successive iterations of the equations 2.3, 2.4, 2.5 or 2.6. As a result, propensities change slowly when they are close to 1 or close to 0, but change more rapidly at intermediate values. We believe that this is biologically plausible, but other relationships might exist and are currently being explored.

3. Results

The principal factors that affect the behaviour of the simulation are the rates of learning λ (increasing propensity) and forgetting ϕ (decreasing propensity). To simplify this initial analysis we studied the dynamics of task allocation where only two tasks are present, and the learning and forgetting rates, λ and ϕ , are manipulated. Each simulation involves twenty initially identical individuals, and the following parameters were universal: resting propensity level, R , 0.2; rate of task accumulation, 5 items per task per timestep; starting propensities, 0.2; density parameter, α , 50.

3.1. INDIVIDUAL BEHAVIOUR

A range of individual responses to these conditions may be exhibited according to the values of learning and forgetting. When learning is rapid relative to

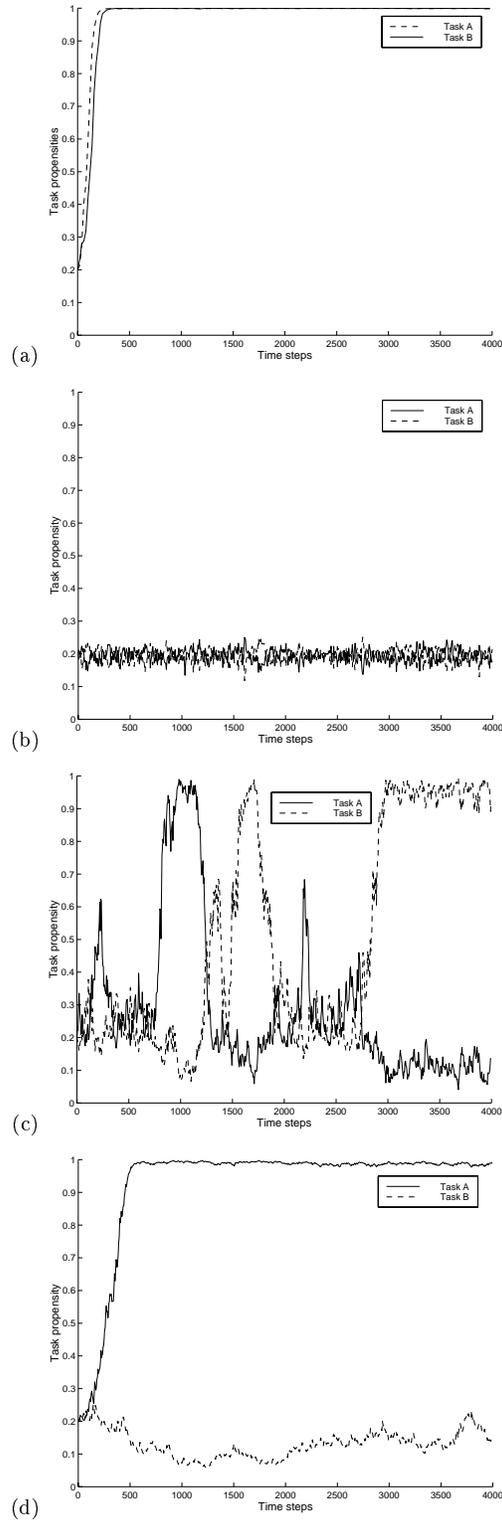


Figure 1. Individual task propensities against time for a range of learning (λ) and forgetting (ϕ) rates: (a) $\lambda = 0.199$, $\phi = 0.0066$; (b) $\lambda = 0.073$, $\phi = 0.1004$; (c) $\lambda = 0.199$, $\phi = 0.0752$; (d) $\lambda = 0.073$, $\phi = 0.0206$.

forgetting, individuals exhibit behaviour such as that shown in Figure 1(a). The individual's propensities for both tasks rise rapidly and stabilise at close to 1, implying that the individual will perform almost every task it encounters. When individuals forget at a greater rate, as in Figure 1(b), their propensities for both tasks never increase significantly above the resting level of 0.2. These individuals rarely perform tasks of either type. In certain areas of parameter space, however, individuals can specialise on one task for variable periods of time (compare Figure 1(c) with Figure 1(d)).

3.2. POPULATION BEHAVIOUR

Figure 2(a) shows the population average propensity for task performance as a function of the rates of learning and forgetting by individuals. The upper plane is characterised by learning rates that are high compared with forgetting rates; the general trend in this region is for agents to perform any task that they encounter (Figure 1(a) exemplifies individual behaviour under these conditions). The lower plane is characterised by learning rates that are lower or only moderately higher than forgetting rates; the general trend in this region is for agents to perform very few of the tasks that they encounter (Figure 1(b) exemplifies individual behaviour under these conditions). In the transition zone between these two regions, intermediate states are found.

Figure 2(b) shows specialization (i.e. the tendency to perform one task more than the other) as a function of the rates of learning and forgetting by individuals (the parameter range for learning and forgetting is identical to that shown in Figure 2(a)). At one end of the specialization zone, that is when learning is slow, specialization tends to be stable (as exemplified by Figure 1(d)). At the other end of the zone, where learning is fast, individual specializations are transient (see Figure 1(c)).

Figure 3 explores the ability of individuals within a population to respond to the introduction of a second task after a period in which they have encountered only one task. When the second task is initially introduced, none of the individuals in the group have encountered it previously and consequently they all have extremely low propensities for performing it. As they begin to encounter the second task, however, their propensities gradually increase until eventually the second task is performed at an equal rate to the first. The time taken to reach this point depends upon their learning and forgetting rates, and Figure 3 shows the time elapsed between the introduction of the second task and the point at which the second task is performed at a rate close to that of the first, across the same range of learning and forgetting rates used in Figure 2. This value is a measure of responsiveness: the shorter the elapsed time, the more rapidly indi-

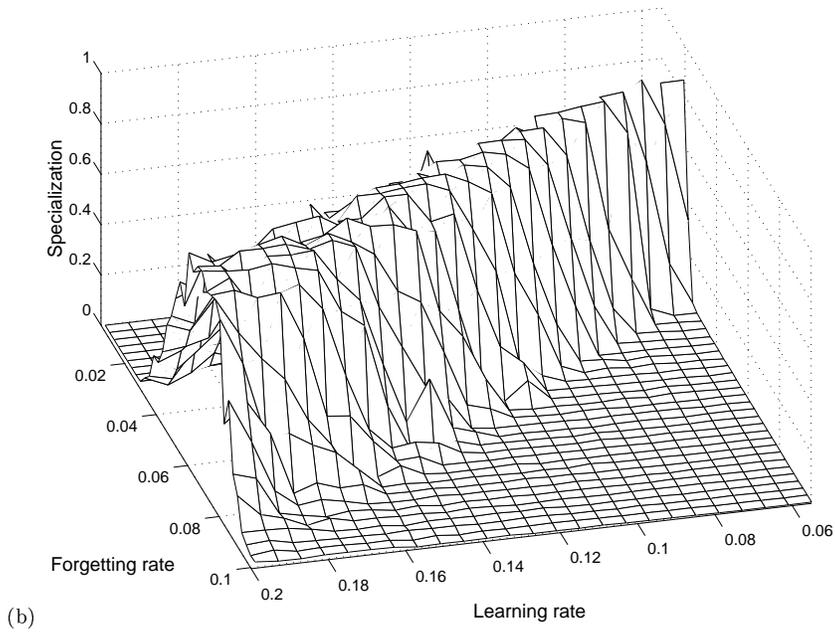
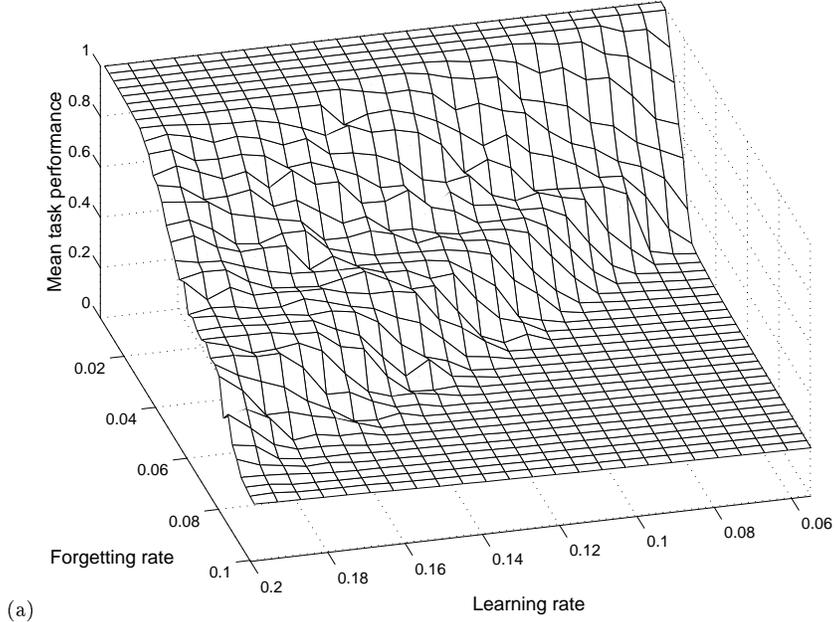


Figure 2. Collective responses across learning (λ) and forgetting (ϕ) parameter space. In both cases the z-axis represents mean values taken over the course of 500 timesteps, after the simulation had been allowed to run for 3500 timesteps. (a) Mean task performance, measured as the mean number of task items dealt with per agent per timestep. (b) Specialization, measured as the mean of the differences between each agents' propensities for the two tasks, $\frac{\sum_{i=1}^n |P_{iA} - P_{iB}|}{n}$ where n is the number of agents (equal here to 20) and P_{iA} and P_{iB} are the agent propensities for tasks A and B.

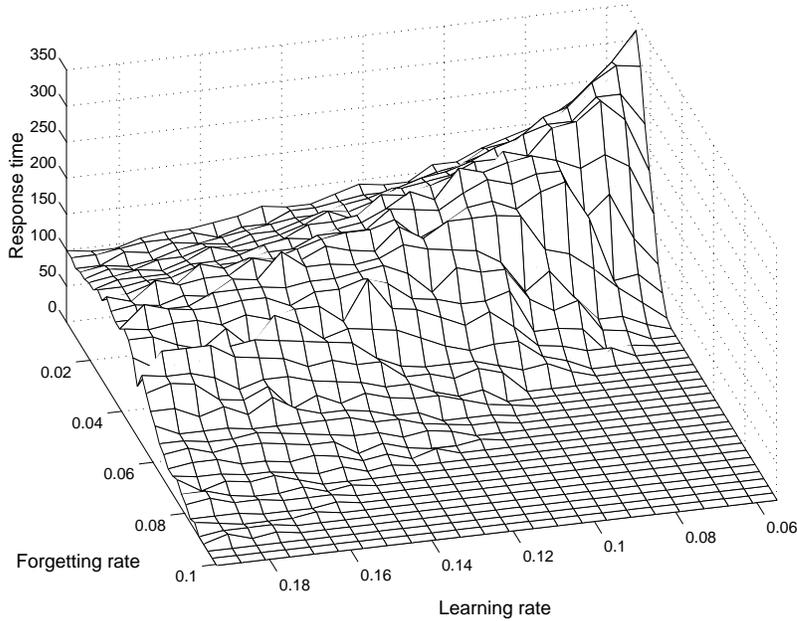


Figure 3. Collective responses across learning (λ) and forgetting (ϕ) parameter space. The simulation was run for 4000 timesteps with only task A present, at which point task B was introduced. The z-axis indicates the time taken before the rate (per agent per timestep) at which task B was performed approached (to within 0.2) the rate at which task A was performed.

viduals are responding to the change in conditions. However, it should be noted that the extremely low area of the graph associated with high forgetting rates is not indicative of a rapid response. This is because when individuals have a high forgetting rate they are incapable of learning even a single task (i.e. their propensities for the first task remain close to the resting level of 0.2); propensities for the second task were at the same resting level of 0.2 before its introduction and consequently little or no time elapsed before both tasks began to be performed at the same (very low) level. This graph shows that the ability to respond to change is associated with high values of both learning and forgetting.

4. Discussion

Our model shows that both generalization and specialization may occur in biological populations as a result of learning and forgetting, and that specialization is associated with a restricted range of parameter space. It further reveals a classic trade-off between stability and responsiveness.

Specialization is common in nature, both in the form of genetic predisposition or adaptation to a task, and in the form of behavioural specialization amongst potential alternative tasks. In this paper we examine the latter, which is much more labile allowing organisms to respond rapidly to their environment. Examples of behavioural specialization include prey specificity in predators (Begon *et al.*, 1990), flower specificity in pollinators (Heinrich, 1979), and task specificity in social insects (Hölldobler and Wilson, 1990; Bourke and Franks, 1995).

There are, however, costs to specialization due for example to increased search time (Krebs and Davies, 1993). Our model incorporates the effects of search time, since specialists ‘waste’ time steps rejecting task items. Figure 2 shows this cost of increased search time (the area of specialization in Figure 2(b) corresponds to the area of decreasing task performance in Figure 2(a)).

The costs of specialization beg the question why it is found so frequently in nature. One answer is that these costs may be offset by efficiency benefits through improved handling of tasks (Krebs and Davies, 1993). Since we do not model efficiency of task performance, this cost is not offset in our model. However, we can predict from our results that where behavioural specialization occurs in nature, organisms are likely to be reaping sufficient benefits from improved handling efficiency to offset the costs of increased search time.

The most likely cause of improved handling efficiency is learning (in the sense of skill refinement). Specialization will be favoured if individuals are not able to learn tasks concurrently, as can occur due to cognitive limitations. Specialization will also be favoured if the costs of learning a second task (incurred because time spent learning a second task is time that could be used to carry out a first task) are greater than the benefits. For simplicity, we have looked only at two tasks here, but the same principle applies wherever organisms are more efficient if they learn only a subset of possible tasks. A well-studied example of this is specialization among flower types by bumblebee foragers. Heinrich (1979) describes the way in which bumble bees learn to cope with different flower morphologies in the search for nectar and pollen. An interesting case, in which specialization is favoured by physiological as well as by behavioural adaptation to a task, is that of the digestive physiology of mallard ducks. It has been shown that these ducks have an increased digestive efficiency when they specialize on a particular food type (Miller, 1975, cited in Begon *et al.*, 1990).

Classical behavioural ecology models have shown, with respect to dietary breadth, that generalists should be expected to occur when the ratio of energy gained per unit handling time is the same for all items, or when search times are extremely long (Krebs and Davies, 1993). Such generalization may also be favoured when there is no significant cognitive limitation to learning tasks concurrently, or when there are no efficiency gains to be made through skill refinement.

Where specialization occurs, our model predicts a trade-off between stability and responsiveness. The population of agents (workers, predators or pollinators) can respond rapidly to the introduction of a new opportunity (task, prey species, flower type), but only if they have high learning and high forgetting rates (see Figure 3). The penalty of such behaviour is that such individuals will rarely specialize on one task for long. Typically they will flip stochastically from one task to another (see Figure 1(c)). In real biological situations this inconsistency would be likely to incur costs: efficiency gained from specializing and developing skills with certain types of item might be thrown away in too rapid switching to alternatives. The penalty of the opposite strategy (that is, stable specializations associated with lower learning and forgetting rates) is that in a changing environment, individuals will adjust their behaviour only slowly.

It is also notable that the area of parameter space where specialization occurs (Figure 2(b)) is also associated with slower responsiveness (Figure 3). This suggests that jacks of all trades, although they may be masters of none, are more likely to be successful opportunists.

There is very good evidence from both vertebrate and invertebrate predators for switching between prey types according to their relative density (Lawton *et al.*, 1974; Murdoch and Oaten, 1975; Murton, 1971; for review see Begon *et al.*, 1990, chapter 9). One traditional hypothesis for such behaviour is that predators form search images (Tinbergen, 1960; but see also Guilford and Dawkins, 1987; Giraldeau, 1997). The notion of a search image is that an organism forms a mental image of a cryptic prey type upon successive encounters and as a consequence tends to be less aware of other prey types. This implies that if the prey for which a predator has a search image becomes very rare, the search image is progressively forgotten, and also that search images are exclusive (a cognitive limitation).

There is also good evidence of switching behaviour in pollinators. Individual bees switch their preferences in response to changing relative abundance of flower types (Heinrich, 1979). For more recent work on bumble bee decision making during foraging, see Cartar (1992), Dukas and Real (1993), Dukas and Waser (1994). Rissing (1981) has shown that individual workers in seed harvesting ants also show preferences for particular seed types and switching behaviour. For

an example of switching behaviour in a non-social pollinator, see Goulson *et al.* (1997).

All of these examples emphasize the advantages of maintaining a specialization whilst a task remains available, and of being able to switch when circumstances change. The importance of individuals being able to respond to a changing environment suggests why in social insect colonies with workers that are physically polymorphic, the least specialized workers are always in the majority. In such cases, extreme physical castes are hard-wired for particular roles and therefore the ability of a colony to respond to a changing environment depends on having large numbers of generalists who can specialize behaviourally according to the needs of their colony (Oster and Wilson, 1978; Tofts and Franks, 1992; Bourke and Franks, 1995).

In solitary organisms, members of a population switch according to their own needs; in a population of workers in a eusocial colony switching can occur that benefits the entire community. If one viewed a colony of social insects exhibiting this trait, decisions might appear to be taken at a global level, but in reality this global behaviour may arise from independent, local decisions by individuals. An alternative model for social insects would have been to consider individuals as having thresholds and that there are global stimuli that emanate from each of the tasks. If the stimulus is greater than this fixed point, then every individual with a threshold below the stimulus would perform the behaviour (see for example Theraulaz *et al.* (in press)). For increased generality, in the model described in this paper, we have adopted an approach based purely on local stimuli.

Our goal in this paper has been to explore in very general terms the dynamics of specialization and generalization in biological populations. In order to achieve some generality, we have deliberately kept our model simple. More specifically, we have excluded explicit spatial considerations in this first version of the model. (Clearly if different tasks, resources or prey types were spatially segregated and agents had restricted patterns of movement then tendencies to specialization could be greatly enhanced.) In the model, learning by the agents is a form of positive feedback and forgetting is a form of negative feedback, and hence our modelling can be seen as an exploration of stability versus responsiveness in terms of the relative magnitude of positive and negative feedback. The model is highly abstract, but for this very reason has revealed potential similarities among a wide range of complex biological systems.

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References

- Begon, M., Harper, J.L. and Townsend, C.R. (1990). *Ecology: Individuals, Populations and Communities*. Blackwell Scientific Publications, Boston.
- Bourke, A.F.G. and Franks, N.R. (1995). *Social Evolution in Ants*. Princeton University Press, Princeton.
- Cartar, R.V. (1992). Adjustment of foraging effort and task switching in energy-manipulated wild bumblebee colonies. *Anim. Behav.* **44**, 75–87.
- Cosmides, L.M. and Tooby, J. (1981). Cytoplasmic inheritance and intragenomic conflict. *J. theor. Biol.* **89**, 83–129.
- Dukas, R. and Real, L.A. (1993). Learning constraints and floral choice behaviour in bumble bees. *Anim. Behav.* **46**, 637–644.
- Dukas, R. and Waser, N.M. (1994). Categorization of food types enhances foraging performance in bumblebees. *Anim. Behav.* **48**, 1001–1006.
- Falconer, D.S. (1981). *Introduction to Quantitative Genetics*, 2nd Edition. Longman, Harlow U.K.
- Giraldeau, L.-A. (1997). The Ecology of Information Use. In: (Krebs, J.R. and Davies, N.B. eds.) *Behavioural Ecology: An Evolutionary Approach*, 4th edition, pp. 42–68. Blackwell Science, Oxford.
- Goulson, D., Ollerton, J. and Sluman, C. (1997). Foraging strategies in the small skipper butterfly, *Thymelicus flavus*: when to switch? *Anim. Behav.* **53**, 1009–1016.
- Guilford, T. and Dawkins, M.S. (1987). Search images not proven: a reappraisal of recent evidence. *Anim. Behav.* **35**, 1838–45.
- Heinrich, B. (1979). *Bumblebee Economics*. Harvard University Press. Cambridge, Massachusetts.
- Hölldobler, B. and Wilson, E.O. (1990). *The Ants*. Springer-Verlag, Berlin.
- Krebs, J.R. and Davies, N.B. (1993). *An Introduction to Behavioural Ecology*, 3rd edition. Blackwell Scientific Publications, Oxford.
- Lawton, J.H., Beddington, J.R. and Bonser, R. (1974). Switching in invertebrate predators. In: (Usher, M.B. and Williamson, M.H. eds.) *Ecological Stability*. Chapman and Hall, London.
- MacArthur, R.H. (1955). Fluctuations of animal populations and a measure of community stability. *Ecology* **36**, 533–536.
- May, R.M. (1973). *Stability and complexity in model ecosystems*. Princeton University Press, Princeton.
- Maynard Smith, J. and Szathmáry (1995). *The Major Transitions in Evolution*. Oxford University Press, Oxford.
- Medawar, P.B. (1957). *The Uniqueness of the Individual*. Methuen, London.
- Miller, M.R. (1975). Gut morphology of mallards in relation to diet quality. *Journal of Wildlife Management* **39**, 168–173.
- Murdoch, W.W. and Oaten, A. (1975). Predation and population stability. *Advances in Ecological Research* **9**, 1–131.
- Murton, R.K. (1971). The significance of a specific search image in the feeding behaviour of the wood pigeon. *Behaviour* **40**, 10–42.
- Oster, G.F. and Wilson, E.O. (1978). *Caste and Ecology in the Social Insects*. Princeton University Press, Princeton.
- Pimm, S.L. and Lawton, J.H. (1977). The number of trophic levels in ecological communities. *Nature* **268**, pp.329–331.

- Ridley, M. (1993). *Evolution*. Blackwell Scientific Publications, Boston.
- Rissing, S.W. (1981). Foraging specializations of individual seed-harvester ants. *Behav. Ecol. Sociobiol.* **9**, 149–152.
- Smith, A. (1776). *The Wealth of Nations*, Books I–III. Reprinted 1986 (A. Skinner, ed.). Penguin, Harmondsworth, U.K.
- Theraulaz, G., Bonabeau, E. and Deneubourg, J.-L. (in press). Response threshold reinforcement and division of labour in insect societies. *Proc. R. Soc. Lond. B*.
- Tinbergen, L. (1960). The natural control of insects in pinewoods. 1: Factors influencing the intensity of predation by songbirds. *Archives Néerlandaises de Zoologie* **13**, 266–336.
- Tofts, C. and Franks, N.R. (1992). Doing the right thing: ants, honeybees and naked mole-rats. *Trends in Ecology and Evolution* **7** (10), 346–349.