with 7000 inhabitants, was at risk.

Several actions were undertaken to protect the village. A 234-m-long and 21-m-high dam was built out of 370,000 m^3 of earth, scoriae, and stones. The dam contained the lava and was breached after about 1 month. Three additional smaller earthen barriers were built to slow the flow toward Zafferana.

The main effort consisted of several attempts to stop the advance of the lava front by the diversion of the flow out of its natural and extensively tunneled channel. The main intervention was made at an elevation of 2000 m in an almost inaccessible zone with the extensive use of helicopters. Initially an attempt was made to plug the entrance of a tunnel by dumping concrete blocks, antitank obstacles (hedgehogs), and blasted portions of a solid levee into it. The interventions caused the partial obstruction of the tunnel, which made part of the lava pour out into the adjoining Valle del Bove, with the consequent halt of the advancing front. However, benefits lasted only 2 weeks, after which the lava started again its slow advancement toward the outskirts of Zafferana.

The final successful intervention was carried out from 27 to 29 May. An artificial channel was dug departing from the natural one. The solid separation levee was thinned to 3 m and blasted by 7000 kg of explosive. Two-thirds of the lava then spontaneously flowed into the artificial channel. A total diversion was obtained when the tunnel was plugged with 230 m^3 of lava boulders. The lava front, only 850 m from Zafferana, stopped at last. In June 1992, the effusion rate was halved from 30 to 15 m^3/s, and with the reduced thrust, the lava was no longer capable of long-distance runs (*8*). The eruption ended on 30 March 1993 after 473 days of continuous lava flows. It was probably the largest eruption of Etna in the last 300 years, covering about 7 km^2 with more than 250 million cubic meters of lava.

The European Science Foundation has recently promoted a scientific program, called EVOP (European Volcanological Project), that gathers all the expertise spread across Europe and focuses it on the knowledge of the internal plumbing system of volcanoes, the mechanism of eruptions, and eruption forecasting. One major problem of volcanological research is that volcanoes are different in terms of plumbing systems and active behavior; therefore, transfer of knowledge from one volcano to another is not straightforward. Europe has the advantage of the availability of a virtually complete spectrum of volcano types in different structural settings. Six were chosen as laboratory volcanoes with the rationale of covering that spectrum as widely as possible. They are Mount Etna (Italy), Krafla (Iceland), Piton de la Fournaise (Réunion Island, France), Teide (Canary Islands), and Furnas (the Azores, Portugal). The project includes the formation of a multidisciplinary team of volcano experts for immediate response to a volcanic alert.

Although advances have been made in Europe, some methodologies are still waiting to be used at their full potential, even on such threatening volcanoes as Mount Vesuvius and Phlegraean Fields. High quality seismic exploration, such as that employed for oil research, advanced seismic tomography, and deep drilling, are necessary to improve our knowledge of these volcanoes.

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Evolving in a Dynamic World

Andrew F. Read and Paul H. Harvey

In the 1980s, a new prominence for organismic biology was marked by the emergence of behavioral ecology, a field spearheaded by two British biologists, J. Krebs and N. Davies. Behavioral ecology consists in large part of applying optimality models to help understand why animals behave as they do. Those models often depend on the frequency of certain reproductively significant events, but recent work suggests that this evolutionary approach may profitably be broadened into the ecological domain by incorporating density as well as frequency dependence.

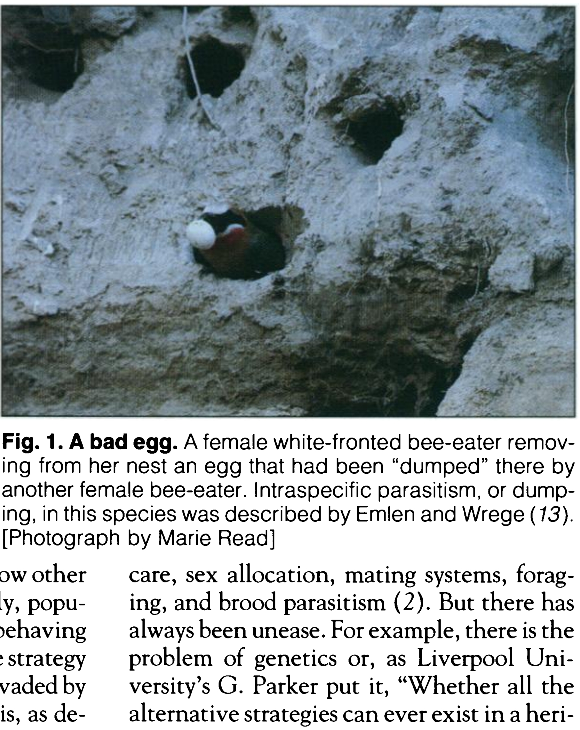

Fig. 1. A bad egg. A female white-fronted bee-eater removing from her nest an egg that had been "dumped" there by another female bee-eater. Intraspecific parasitism, or dumping, in this species was described by Emlen and Wrege (*13*). [Photograph by Marie Read]

Behavioral ecology often demonstrates that the evolutionarily favored behavior for one individual in a population depends on how other individuals are behaving. Eventually, populations of individuals will end up behaving according to an evolutionarily stable strategy (ESS), that is, one that cannot be invaded by others. For example, an ESS analysis, as developed by J. Maynard Smith (University of Sussex) and G. Price (University of London), for understanding why animals do not always escalate fights (*1*) depends on defining a set of available strategies and then seeing which strategies persist at equilibrium after specifying an optimization principle and a starting point. This approach has unraveled several biological conundrums, including aspects of aggressive behavior, parental care, sex allocation, mating systems, foraging, and brood parasitism (*2*). But there has always been unease. For example, there is the problem of genetics or, as Liverpool University's G. Parker put it, "Whether all the alternative strategies can ever exist in a heritable form in real populations is an important question, but," he added comfortingly, "that should not deter us from considering what would happen if they could" (*3*)! Just as behavioral ecology must take on board genetic realism in order to broaden its scope, so it cannot much longer ignore population dynamics. The fitness costs and benefits of many reproductive strategies are likely to be density- as well as frequency-dependent.

Intraspecific brood parasitism, a topic increasingly studied by behavioral ecologists (*4*), illustrates the possible importance of both density and frequency dependence in ESS studies. Brood parasites, typically birds

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A. F. Read is in the Division of Biological Sciences, University of Edinburgh, West Mains Road, Edinburgh EH9 3JT, United Kingdom. P. H. Harvey is in the Department of Zoology, University of Oxford, South Parks Road, Oxford OX1 3JT, United Kingdom.

or insects, parasitize the parental care of conspecifics by laying their eggs in the nests of others. These eggs are usually less likely to produce a breeding adult, because eggs are frequently dumped at inappropriate times during the nesting cycle or rejected by hosts (Fig. 1). They may also reduce host fitness, as when, for example, host eggs are exchanged for parasite eggs or hosts must raise more offspring than is optimal. Under these conditions, population size not only determines the selective benefits of dumping (for example, birds unable to obtain nests may have only egg-dumping as a reproductive option), but is itself determined by its frequency.

S. Nee and R. May (*5*), working at the University of Oxford, attempt to examine this intertwined density and frequency dependence by considering a situation in which the population size of a bird species is limited initially by the availability of nest sites. Birds with nests lay only in those nests, and birds that fail to get nest sites dump their eggs randomly in the nests of others; these eggs reduce host fitness. The intimacy of the ecological and the evolutionary is clearly illustrated by Nee and May's first result. Consider the situation where individual parasites, freed from the costs of building a nest, lay more eggs than do individual hosts. If this difference in fecundity is sufficient to offset the lower success of parasitic eggs relative to host eggs, parasitism no longer adds up to making the best of a bad job, and hosts would be better off abandoning their nests and becoming professional parasites. Nee and May point out that this situation is evolutionarily unstable, since professional parasites would invade a population of facultative parasites. However, if parasites are more fecund than their hosts but their eggs are a lot less successful, then the population crashes. Consequently, most birds get nest sites the next year, there are few best-of-a-bad-job parasites, and the population grows.

Combining alternative scenarios, Nee and May demonstrate analytically that there is a threshold ratio of the number of eggs a parasite produces relative to host clutch size above which it is impossible to have both population dynamic stability and evolutionary stability. There may be one or the other, or even neither, but it is impossible to have both. Below this threshold there is also a large region of parameter space where birds would be better off giving up nest-building and becoming full-time parasites. Because of the negative effects of dumping on hosts, this can occur even if parasitic eggs are much less successful than host eggs. Once professional parasites start to invade a population, the number of nesters may be driven below the number of nest sites. What happens next depends on the intensity of parasitism experienced by hosts. Extinction can result, or the population can oscillate above and below the number of nest sites, with no equilibrium.

Nest site limitation is one of the most stabilizing classes of population-regulating mechanisms, but in this instance the natural evolution of reproductive strategies has the potential to destabilize the population dynamics. Likewise, these results clearly point to the potential problems of ignoring population dynamics in frequency-dependent evolutionary analyses. If characters being considered are themselves density-regulating factors, or if population density affects phenotypes in different ways, then fitness functions need to be explicitly density-dependent in addition to any frequency dependence.

These models also suggest one novel reason for the apparent absence of professional intraspecific brood parasites. The negative consequences of superparasitism are more severe for professional parasites than for facultative parasites (nesters with surplus eggs or birds unable to get a nesting site), for whom any success through dumping may be better than nothing. As a result, superparasitism by facultative parasites can be maintained by selection at a frequency above that at which professional parasitism can be sustained. Just how effective facultative dumpers are at immunizing populations against the invasion of professional parasites depends on the dispersion of parasite attacks: any clumpiness concentrates the effects of superparasitism and makes the necessary conditions even more stringent.

Nee and May suggest that the evolutionary trajectories followed by any species could be examined with models that explicitly specify relevant details of natural history. Just such a model has recently been described for the Barrow's goldeneye *Bucephala islandica* (*6*), which led its authors, J. Eadie and J. Fryxell, also to emphasize how the conclusions of the ESS models can be altered by incorporating population dynamics. For example, an analysis of brood parasitism in two populations of digger wasps (*7*) predicted correctly the frequency of brood parasites in only one of two populations studied. The other population subsequently went extinct. Eadie and Fryxell (*6*) suggest that the failure of the analysis in that population may have been due to population differences in demographic factors. As Nee and May (*5*) point out, the relevant differences in population dynamics, including the local extinction, could have been generated endogenously by the behavioral dynamics alone.

The brood parasitism models outlined above examine temporal changes in parasite frequency and in population density. But populations are not homogeneous in space, and that spatial heterogeneity that is found in natural populations is often considered to arise from environmental heterogeneity. Such a conclusion may be unwarranted. Recent work by M. Hassell and his colleagues (*8, 9*) at the University of London's Imperial College examines both temporal and spatial dynamic change in host-parasitoid (parasitoids are parasitic insects with a free-living stage in their life cycle) systems in a model world consisting of identical habitat patches. Within each patch, the population dynamics of host and parasite are unstable, with local extinction the inevitable outcome. Now add the biologically realistic detail that dispersal of hosts and parasitoids occurs only between localized patches, rather than to any patch. If the array of patches is large enough, this purely deterministic system generates many spatial patterns that may be indistinguishable from those caused by habitat heterogeneity. A common outcome is the formation of spiral waves, where patch densities vary through time with a wave of high-density hosts spiraling out from a central focus pursued by a high-density parasite wave (Fig. 2). Around these traveling waves, low-density (or empty) patches exist. These waves can be dynamically stable, or they can disintegrate and reform to create spatial chaos.

How evolution proceeds in Hassell and colleagues' dynamic world is only beginning to be explored. For example, Boerlijst and co-workers (*10*) at the University of Utrecht have analyzed what is essentially a two-species competition model by setting up dynamically stable spiral waves of host and parasi-

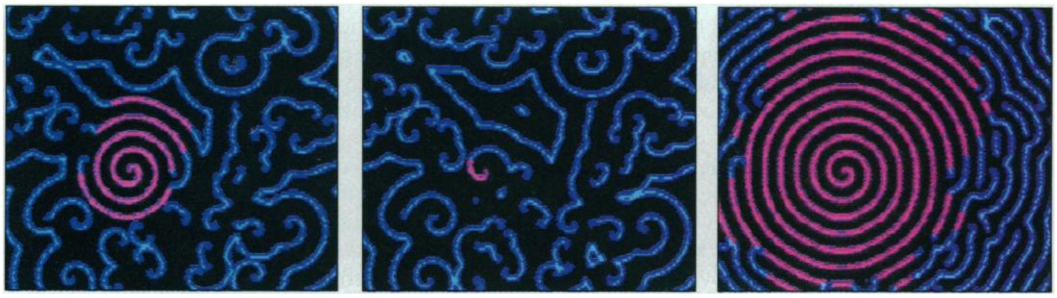

Fig. 2. Paradoxically spiraling parasitoids. When less efficient parasitoids (purple) are introduced into a field of patches containing high-efficiency parasitoids (blue), they spread with time and take over the previously stable spirals (left to right). Brighter color corresponds to abundance. [Reprinted with permission from (*10*), © The Royal Society of London (1993)]

toid. Into this they introduce a population of mutant parasites that have different rates of locating hosts and converting them into offspring (efficiency) (Fig. 2). They find that even though selection (competition) within a patch favors parasites with higher efficiency, lower efficiency parasites can be maintained. This is because greater host dispersal occurs where hosts are regulated by lower efficiency parasitoids. The wave front is thus less inhibited by local extinction of the host. Faster rotating spirals gradually expand to take over the domain of slower ones and the less efficient parasitoids dominate (Fig. 2). Hence the direction of within-patch selection is contradicted by what Boerlijst and co-workers term "between spiral" selection. Such an outcome is reminiscent of the consequences of group structure on the outcome of selection much studied for the last few decades (*11*, *12*). And it was Wynne-Edwards' suggestion that group selection was responsible for population regulation and nonviolent contests that set Price and Maynard Smith to developing their ESS models in the first place.

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Supramolecular Chemistry

Jean-Marie Lehn

When a substrate binds to an enzyme, a drug sticks to its target, or signals propagate between cells, highly selective interactions occur between the partners to control the process. Supramolecular chemistry is concerned with the study of the basic features of these interactions and with their implementation in specially designed nonnatural systems.

For more than 150 years, since the synthesis of urea by Friedrich Wöhler in 1828, molecular chemistry has developed a vast array of highly sophisticated and powerful methods for the construction of ever more complex molecular structures by the making or breaking of covalent bonds between atoms in a controlled and precise fashion. The time has come to do the same for noncovalent intermolecular forces. Just as there is a field of molecular chemistry based on the covalent bond, there is a field of supramolecular chemistry, the chemistry of molecular assemblies and of the intermolecular bond. It is "chemistry beyond the molecule," whose objects are supramolecular entities, supermolecules possessing features as well defined as those of molecules themselves (*1*, *2*).

Supramolecular chemistry is a highly interdisciplinary field of science covering the chemical, physical, and biological features of chemical species of higher complexity, that are held together and organized by means of intermolecular (noncovalent) binding interactions. This relatively young area has been rapidly defined, conceptualized, and structured into a coherent system. Its roots extend into organic chemistry and the synthetic procedures for receptor construction, into coordination chemistry and metal ion–ligand complexes, into physical chemistry and the experimental and theoretical studies of interactions, and into biochemistry and the biological processes that all start with substrate binding and recognition. A major feature is the range of perspectives offered by the cross fertilization of supramolecular chemical research, owing to its location at the intersection of chemistry, biology, and physics. Such wide horizons are a challenge and a stimulus to the creative imagination of the chemist.

The field started with the selective binding of alkali metal cations by natural (*3*) as well as synthetic macrocyclic and macropolycyclic ligands, the crown ethers and cryptands (*1*, *4*). This led to the emergence of molecular recognition as a new domain of chemical research that expanded over other areas and became supramolecular chemistry (*1*, *2*). It underwent explosive growth with the development of synthetic receptor molecules of numerous types for the strong and selective binding of cationic, anionic, or neutral complementary substrates of organic, inorganic, or biological nature by means of various interactions (electrostatic, hydrogen binding, van der Waals, and donor-acceptor). Molecular recognition implies the (molecular) storage and (supramolecular) retrieval of molecular structural information. Many types of receptor molecules have already been explored (crown ethers, cryptands, spherands, cavitands, calixarenes, cyclophanes, cryptophanes, and so forth) (*4*, *5*). Still others may be imagined for the binding of complementary substrates of chemical or biological significance; for instance, for the development of substrate-specific sensors or for the recognition of structural features in biomolecules (nucleic acid probes, affinity cleavage reagents, enzyme inhibitors, and so on).

The combination of recognition features with reactive functions generates supramolecular reagents and catalysts that operate in processes involving two main steps: substrate recognition followed by its transformation into products. Because of their relationship with enzymatic catalysis, they present protoenzymatic and biomimetic features. By nature, they are abiotic reagents that may perform the same overall processes as enzymes without following the same mechanistic pathways. More importantly, they may also effect highly efficient and selective reactions that enzymes do not perform. This represents a very important area for further development, which may lead to a range of reactive receptor molecules combining substrate specificity with high reactional efficiency and selectivity. Much work remains to be done that should contribute very significantly to the understanding of chemical reactivity and to its application in industrial processes.

Suitably modified receptors act as carriers for the selective transport of various types of substrates through artificial or biological membranes. Further developments may concern, for instance, the construction of selective membrane sensors or the transport of drugs through biological barriers, which may include targeting if suitable target selective recognition groups are introduced.

Recognition, reactivity, and transport represent the three basic functional features of supramolecular species. A further important line of development concerns the design of supramolecular devices built on photoactive, electroactive, or ionoactive components, operating with photons, electrons, and ions, respectively. Thus, a variety of photonic devices based on photoinduced energy and electron transfer may be imagined (*2*, *6*). Molecular wires, ion carriers, and channels facilitate the flow of electrons and ions through membranes. Such functional entities represent entries into molecular photonics, electronics, and ionics that can be used for stor-

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The author is in the Collège de France, Paris, and Université Louis Pasteur, Strasbourg, France.