in poorly informed and often mischievous struggles over 'territory'. Leaders, who are not given to such posturing and squabbling, should recognize the complementary nature of all six varieties. They should find ways of fostering mutualistic or cooperative interactions. Above all, any emerging mutualism should serve the interests of humanity as informed by a through-going Biospheric Ethic.

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XVI

Ecological Phenomena in Evolutionary Perspective

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SEX RATIO

A colleague who was preparing for the first time to teach elementary population biology once asked me, as a veteran, what I covered in such a course. I quickly rattled off a long list, including an examination of why sex ratios were frequently near to 50:50. He looked at me somewhat incredulously, as though the answer to this question was trite, and said 'Well, we all know that half the sperm carry an *x* chromosome and the other half carry the *y*.' In the manner of many non-evolutionarily-oriented biologists, he was quite satisfied with a *functional* explanation for sex ratios near equality.* In the above conversation I was, of course, contemplating the *evolutionary* basis for sex ratios. Our time-scales were different: my colleague's answer was framed in terms of ecological time (or 'now' time, within the life-spans of individuals), whereas mine would be couched in evolutionary time involving many generations.

The late Sir Ronald Fisher seems to have been the first to appreciate the evolutionary basis for a sex ratio near equality (Fisher, 1930). Fisher simply pointed out that, regardless of the present sex-ratio, each and every generation derives exactly half of its autosomal genes from maternal ancestry while the other half come from the paternal side. As a result, the aggregate of all males must contribute exactly as many genes as that of all females, whatever the current sex-ratio. Hence if, say, females outnumber males, an

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* Some have argued that sex ratios of 50:50 are wasteful in species where one male can service more than a single female, and that sex ratios in such species should therefore be biased towards females. Darwin (1871) suggested that sex ratios near equality might be selected to minimize intrasexual fighting over mates. Such fallacious group-selectionist arguments are, however, not considered further here.

average female will contribute less to the next generation than an average male, sons being accordingly more valuable than daughters. Fisher concluded that the optimal family tactic is to allocate precisely half of any parental investment to sons and the other half to daughters: provided the population is at equilibrium, this tactic cannot be beaten—it is what Maynard Smith (1972, 1974) calls an 'evolutionarily stable strategy.'

Needless to say, if the population is out of equilibrium, investing in an excess of the under-represented sex is always profitable; this, in turn, drives the population sex-ratio back towards its equilibrium in a frequency-dependent manner. Fisher (1930) assumed that each male has the same probability of mating as any other (likewise, all females are assumed to have equal chances of breeding), so that his argument does not depend on competition for mates in any way. (Note that Fisher's powerful argument is framed in terms of parental investment rather than in numbers *per se;* if offspring of one sex cost parents more to produce than progeny of the other sex, fewer of the more expensive sex should be produced.)

Human sex-ratios at birth, in fact, are not exactly 1 to 1, but deviate towards a slight excess of sons (though slight, this skew is significant in a statistical sense provided that samples are large enough). My colleague could, of course, 'explain' this uneven primary sex-ratio in mechanistic terms—e.g. due to their lighter weight, pH tolerance, or whatever, *y* sperms enjoy a higher mobility or greater survivorship, and hence collectively fertilize more ova, than do *x* sperms. Fisher (1930) provided an evolutionary explanation for the observed patterns: infant mortality in humans is higher among sons than daughters. Given this innate differential mortality (which itself must stem from differences in sexual selection) during the period of parental care, investment in offspring of the two sexes can be equalized only by beginning parental care with an excess of sons and ending the period of parental care with an excess of daughters.

Avian Migration

Let us now consider another but quite different question: 'Why do north-temperate-zone migratory birds fly south in the autumn?' A physiologically-inclined biologist would tell us that decreasing day-length (photoperiod) causes the pituitary to secrete hormones which alter bird behaviour and increase nocturnal restlessness (Zugenruhe). Eventually, this 'wanderlust' gets the upper hand and the birds head south.

In contrast, an evolutionist would explain that, by virtue of reduced winter mortality, those birds that flew south lived longer and therefore left more offspring than their non-migratory relatives. Over evolutionary time, intricate patterns of migratory behaviour therefore evolved by means of differential reproductive success.

Colour Patterns

MacArthur & Connell (1966) give another example of these two different ways of approaching biological questions. They ask: 'Why is a Viceroy Butterfly [*Limenitis archippus*] orange?' A mechanistic answer describes the chemical structure of certain pigments and their reflectance properties for orange wavelengths. However, an evolutionary answer is formulated in terms of Batesian mimicry: ancestors of present-day Viceroy Butterflies that produced orange pigments were mistaken for distasteful, warningly-coloured, Monarch Butterflies (*Danaus plexippus*) by avian predators. As a result, orange Viceroys enjoyed higher survivorship and left more offspring than non-orange Viceroys. Over evolutionary time, the resemblance between the mimetic Viceroy and its model, the unpalatable Monarch (*Danaus plexippus*), was improved until it became quite close. MacArthur & Connell (1966) note that an evolutionist need not even be particularly concerned with the precise mechanism by which the resemblance takes place—presumably many different pigments for orange could confer similar phenotypes and thus comparable fitnesses.

Clutch-size in Birds

'Why does a Yellow-shafted Flicker (*Colaptes auratus*) normally lay from 6 to 8 eggs?' In one classic experiment, a female Flicker was induced to lay 71 eggs in 73 days by the simple removal of eggs as rapidly as they were laid, leaving a single 'nest' egg behind (Welty, 1963). Thus such indeterminate layers are capable of laying many more eggs than they usually do.

Once again, the question can be answered at two levels: (1) Somehow, in a manner that is, as yet, poorly understood, the feel of the 'proper' number of eggs against the female's brood-pouch stimulates the anterior pituitary to secrete a prolactin-type of hormone which induces regression of the ovary and initiates incubation behaviour; or (2) from six to eight chicks is the maximal number that the parental birds can successfully feed, such that parents opting for this clutch-size enjoy a greater lifetime reproductive success than do birds that lay either fewer or more eggs per clutch (Lack, 1954; Williams, 1966*b*).

The Functional *versus* the Evolutionary Approach

The functional approach is involved with the immediate *mechanism(s)* by which an event or phenomenon occurs, whereas the evolutionary approach is concerned with what can be called a 'strategy' by which individuals maximize their lifetime production of progeny. Mayr (1961) termed these the 'how?' and 'why?' approaches in biology; Baker (1938) distinguished between the 'proximate' and the 'ultimate' factors influencing an event or phenomenon. These two levels of approach in biology neatly complement each other and a really thorough understanding and appreciation of any biological phenomenon requires both. The strength of the evolutionary approach has been stressed by MacArthur (1961), Orians (1962), and Lack (1965), among others.

A major revolution has occurred in biology during the last half-century, following Fisher's (1930) pioneering efforts towards rigorously applying Darwin's theory of natural selection by differential reproductive success of individual organisms. Before then, most biologists essentially accepted a broad range of biological phenomena as unchanging and even immutable (some biologists still do). The evolutionary approach has provided powerful new insights into the evolution of a wide variety of ecological phenomena (some references to selected major contributions are listed at the end of this paper). These include sex ratios (Fisher, 1930; Kolman, 1960), mating systems (Orians, 1969), social behaviour (Hamilton, 1964; Trivers, 1971, 1974), senescence (Medawar, 1957; Hamilton, 1966; Emlen, 1970), patterns and modes of foraging (Emlen, 1966, 1973; MacArthur & Pianka, 1966; Pianka, 1966; Orians & Pearson, 1979; Huey & Pianka, 1981), reproductive tactics and life-histories (Lack, 1954; Lewontin, 1965; MacArthur & Wilson, 1967; Pianka & Parker, 1975; Pianka, 1976), competitive interactions (Roughgarden, 1976), niche relationships (MacArthur & Levins, 1967; Levins, 1968; MacArthur, 1972), prey–predator interactions (including aspect diversity and plant–herbivore interactions) (Fisher, 1958; Rand, 1967; Ricklefs & O'Rourke, 1975; Feeny, 1976; Lawlor & Smith, 1976; Schall & Pianka, 1980; Futuyma & Slatkin, 1983), and community structure and succession (Levins, 1975; Horn, 1976; Pickett, 1976).

To illustrate the power and utility of the selective approach in ecology, I will outline arguments for the evolution of senescence and for that of optimal reproductive tactics, before concluding by briefly discussing certain pitfalls in applying the evolutionary approach to understanding ecosystems and pointing out some challenging but promising directions for future extensions in evolutionary ecology.

EVOLUTION OF SENESCENCE

The physiological manifestations of ageing have long been of considerable interest, and have received the attention of gerontologists for some time. But the evolutionary basis for senescence was almost entirely neglected until about three decades ago.

Why in fact *do* organisms become senile with age? One might expect quite the opposite, as older organisms have had more experience than young ones, and should have learned how to avoid enemies, have more antibodies, etc. Old organisms should thus be wiser and better adapted, both behaviourally and immunologically, than young ones. Is senescence inevitable? Rigorous application of Darwin's theory of natural selection tells us that Ponce de Leon's vision of eternal youth may forever remain a mirage.

Sir Peter Medawar (1957) made the following rather compelling case for the evolution of senescence. A chemist's laboratory has a stock of 1,000 test-tubes and a monthly breakage rate of 10%. Each month one hundred test-tubes are broken, completely at random, and another one hundred new ones are added to replace them. New tubes are marked with their date of acquisition, so that their age of service in months can be determined later. Every test-tube has exactly the same probability of survival from any one month to the next: 900/1,000 or 0.9. Older test-tubes thus have the same mortality as younger ones, and there is no senility. All test-tubes are—in actual fact to some tiny extent—*potentially* immortal. The probability of surviving for two months is simply the product of the probability of surviving each month separately, or 0.9 times 0.9 ($0.9^2 = 0.81$), while that of surviving for three months is 0.9^3, and the probability of surviving for x months is 0.9^x.

After some years, the population of test-tubes settles down at its stable age-distribution, with 100 aged 0 month, 90 aged 1 month, 81 aged 2 months, ..., 28 aged 12 months, ..., 8 aged 24 months, ..., 2.25 aged 36 months, ..., and so on, with less than one test-tube in age-groups over 48 months, totalling in all 1,000 tubes. (These numbers are merely the *expected* numbers of tubes of a given age; random sampling and stochastic variations will result in some numbers in various age-groups being above, while others will be below, these expected values.) In any case, young test-tubes greatly outnumber older ones. Virtually none are over five years old, even though individual test-tubes are potentially immortal. With the passage of time, increased handling results in almost certain breakage.

To each of the 900 test-tubes surviving at the end of every month, Medawar (1957) assigns an equal share of that month's 'reproduction' (i.e. the hundred new tubes added during that month). Hence each surviving tube reproduces 1/9 of one tube per month. Test-tube fecundity does not change with age, although the proportions of tubes 'reproducing' does. Younger age-groups contribute much more to each month's reproduction than do older ages, simply because there are more of them. However, an individual test-tube at any age has exactly the same expectation of further life and future 'progeny' as a tube at any other age: thus an old test-tube is entirely equivalent to a young tube, and there is still no senescence.

Next, Medawar pretends that these test-tubes have 'genes'. Consider the fate of a mutant whose phenotypic effect is to make its bearer slightly more brittle than an average test-tube. The gene is clearly detrimental, as it reduces the probability of survival and therefore the fitness of its carrier. This mutant is at a selective disadvantage and will eventually be eliminated from the population. Consider now the fate of another set of mutant alleles at a different locus, which control the time of expression of the first gene for brittleness. Different alleles at this second locus alter the time of expression of the brittle gene differently, with some causing it to be expressed early and others late. Obviously, a test-tube with the brittle gene and a 'late' modifier gene is at an advantage over a tube with the brittle gene and an 'early' modifier, simply because the former tube will live longer on the average and hence produce more offspring. Thus, even while the brittle gene is slowly being eliminated by selection, 'late' modifiers will accumulate at the expense of 'early' modifiers.

The later the time of expression of brittleness is, the more nearly normal will a test-tube be in its contribution to future generations. In the extreme, after reproductive value (expectation of future offspring) decreases to zero, natural selection can no longer postpone the expression of a detrimental trait and it emerges as senescence. Traits that have been postponed to old age by selection of modifier genes have effectively been removed from the population gene-pool. For this reason, Medawar (1957) referred to old age as a 'genetic dustbin.' He terms this inevitable process of selection, postponing the expression of detrimental genetic traits, 'recession of the overt effects of an allele'.

Exactly analogous arguments apply to changes in the time of expression of beneficial genetic traits, except that here selection works to move the time of expression of such characters to earlier ages, with the result that bearers benefit maximally from possession of the allele (this is called 'precession of the beneficial effects of an allele'). We are in fact contemplating the process of age-specific selection, which has been analysed more quantitatively by Hamilton (1966) and Emlen (1970).

Interestingly enough, artificial selection for early reproduction in laboratory studies on *Tribolium* beetles resulted in decreased longevity, demonstrating that senescence does in fact evolve (Sokal, 1970; Mertz, 1975).

OPTIMAL REPRODUCTIVE TACTICS

Another aspect of age-specific selection concerns what can be termed an organism's reproductive tactics. Here the question is: 'How much should the organism invest in current reproduction at any given age?' A closely-related question is 'Why invest anything in somatic tissues, organs, and activities, at all?' Somatic tissues are clearly necessary for acquisition of matter and energy; however, an organism's soma is of no selective value except inasmuch as it enhances that organism's lifelong reproductive success. What is needed is a way to measure the present value of an organism's body at a given age in terms of its expectation of future offspring, or its residual reproductive value. To maximize its lifetime contribution to future generations, an optimal organism must, so to speak, weigh its immediate prospects of reproductive success against its long-term future prospects (Williams, 1966*a*, 1966*b*; Pianka & Parker, 1975; Pianka, 1976).

An individual with a high probability of substantial future reproductive success should be more hesitant to risk its soma in current reproductive activities than another individual with a lower expectation of future reproductive success. I envisage a trade-off between current reproduction and expected future reproductive success, with gains in either necessarily reducing the other (Fig. 1). Investment in reproduction often decreases growth and/or survivorship, hence lowering expectation of having future offspring. Each curve in Fig. 1 represents a set of all possible tactics that are open to a hypothetical individual organism at some instant (age) in its lifetime. One of these hypothetical organisms achieves its highest possible current reproductive success by so-called 'big bang' all-out suicidal reproduction, but this

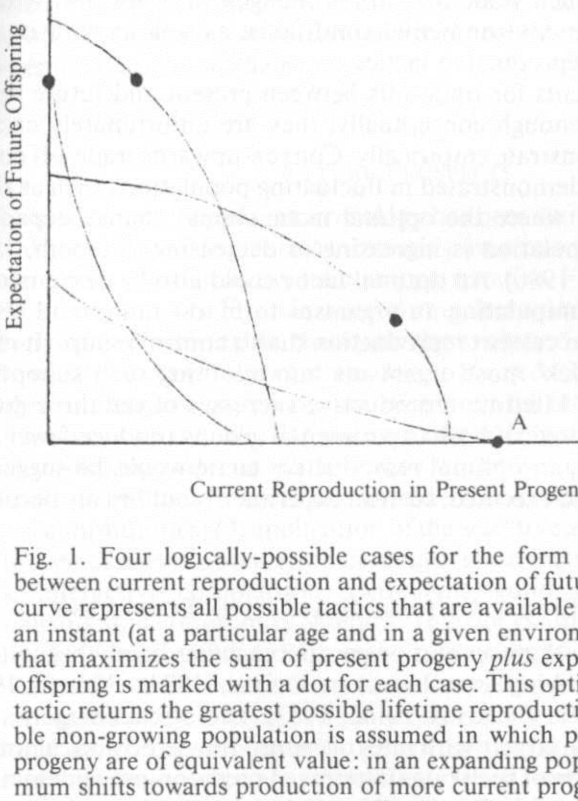

Fig. 1. Four logically-possible cases for the form of the trade-offs between current reproduction and expectation of future progeny. Each curve represents all possible tactics that are available to an organism at an instant (at a particular age and in a given environment). The tactic that maximizes the sum of present progeny *plus* expectation of future offspring is marked with a dot for each case. This optimal reproductive tactic returns the greatest possible lifetime reproductive success. A stable non-growing population is assumed in which present and future progeny are of equivalent value: in an expanding population, the optimum shifts towards production of more current progeny because they are more valuable than future offspring, whereas the reverse is true during a population decline.

tactic necessitates zero future progeny (dot marked A in Fig. 1). This semelparous (one-time reproduction) tactic will be optimal only if the gains in present progeny are greater than any other possible tactic on the curve representing all those available. Conversely, a pre-reproductive individual invests nothing in current reproduction but puts everything into growth and maintenance of its soma, and hence into future reproduction. Again, this tactic will be optimal only if no other possibility yields a greater lifetime reproductive success.

Several different, logically possible forms for such trade-off curves are shown in Fig. 1: concave-upwards ones describe an all-or-none situation, inevitably resulting in semelparity. Convex-upwards curves, however, always favour less than maximal current investment and hence result in iteroparity (repeated reproduction). The algorithm for the optimal tactic is simple enough: maximize the sum of present progeny *plus* the expectation of future offspring at every age. This is equivalent to maximizing reproductive value at all ages, and results in a maximal lifetime reproductive success. Of course, the form of such trade-off curves changes with age and with an organism's immediate environmental conditions, as well as with its past experience and past reproductive tactics.

While these arguments for trade-offs between present and future reproduction seem sound enough conceptually, they are unfortunately exceedingly difficult to demonstrate empirically. Convex-upwards trade-off curves could presumably be demonstrated in fluctuating populations such as those of microtine rodents, where the optimal tactic should change depending upon whether the population is increasing or decreasing (Stenseth, 1978; Stenseth & Framstad, 1980). An optimal tactic could also be demonstrated by experimentally manipulating an organism to invest more (and less in another experiment) in current reproduction than a control group. (It might not prove easy to 'trick' most organisms into adopting such suboptimal reproductive tactics!) Lifetime reproductive successes of the three groups would then be monitored: if both experimental groups produce fewer progeny than the control, an optimal reproductive tactic would be suggested. Properly conceived and executed, such an experiment could easily become a minor classic.

Ecological Efficiency *versus* Stability in Ecosystems

At the ecosystem level, the evolutionary approach has barely begun to be incorporated into thinking (*see*, however, Orians, 1974; Pickett, 1976; Orians & Solbrig, 1977; Orians & Paine, 1983). Ecological energetics has thus far been concerned largely with rates of energy-flow in ecological time—analysis of the evolution of such rates in terms of predator–prey interactions might well prove instructive. It is tempting (but dangerously misleading) to view ecosystems as having been 'designed' for orderly and efficient functioning. However, antagonistic interactions at the level of individuals and populations (especially competition, predation, and parasitism) must frequently impair certain aspects of ecosystem performance.

As one example, consider predator–prey interactions. Natural selection, operating by differential reproductive success of individual prey, presumably favours escape ability, whereas selection acting on individual predators favours efficient capture of prey. Any given prey–predator pair has its own particular stand-off (stalemate?) between these conflicting selective pressures. Predator escape tactics of prey clearly reduce the rate at which materials and energy are transferred to higher trophic levels, thus reducing ecological efficiency. Prey escape abilities are also thought to confer stability on prey–predator systems (Rosenzweig & MacArthur, 1963), hence presumably enhancing community stability. On the other hand, the efficiency with which predators capture and handle their prey, enhances ecological efficiency but reduces the stability of the prey–predator system and hence may decrease community stability. These arguments suggest that a trade-off exists between ecological efficiency and community stability. Moreover, this trade-off of ecosystem properties has its roots in evolutionary interactions between predators and their prey.

Future Prospects

The evolutionary approach in ecology has been quite productive, particularly at the level of populations, though numerous ecological phenomena remain to be viewed in an evolutionary perspective. For example, as pointed out by Colinvaux (1973), tolerance curves have usually been accepted as unchanging and immutable, theory on the evolution of tolerance being virtually non-existent (*but see* Levins, 1969; Huey & Slatkin, 1976).

Other challenging, but promising, directions for future extensions in evolutionary ecology include: (1) analysis of the constraints and interactions between foraging and reproductive tactics; (2) development of theory for the evolution of optimal foraging tactics and niche-breadth in both simple and diverse communities; (3) application of the selective approach to a variety of multi-species coevolutionary phenomena (these include symbiotic interactions, interactive competition coefficients, guild structure, competitive mutualisms, and community assembly [*see*, for examples, Holt, 1977; Lawlor, 1979; Vandermeer, 1984]), and (4) consideration of the influence of population-level phenomena (such as fluctuations in population density and/or reproductive success) on the structure and stability of communities (and *vice versa*). The implications of such considerations and applications at the ecobiome and component ecosystems levels, particularly among dominant and co-dominant plants, should be far-reaching and surely merit investigation.

SUMMARY

Events and phenomena of interest in ecosystemic and allied aspects of ecology can be interpreted and understood at two levels: those two approaches to biology, the functional and the evolutionary, neatly complement each other. A really thorough understanding and appreciation of any ecological phenomenon requires both levels of approach. However, the evolutionary basis of many important aspects of ecology has been widely neglected, particularly at the level of ecosystems. Evolutionary analyses of ecosystems are badly needed, but are exceedingly treacherous to attempt. Classical Darwinian selection at the level of the individual may often favour antagonistic behaviours and interactions that can impair certain aspects of ecosystem performance, such as the efficiency with which energy and materials flow between trophic levels, or, in certain circumstances, the stability of communities.

Rigorous application of the theory of natural selection has provided powerful new insights into theevolution of a variety of ecological phenomena, including sex-ratios, mating systems, social behaviour, senescence, patterns and modes of foraging, reproductive tactics and life-histories, competitive interactions, niche relationships, prey–predator interactions (including aspect diversity and plan–herbivore interactions), community structure, and succession. Selected examples are briefly reviewed that illustrate the strength of the selective approach in population ecology. Some challenging, but promising, directions for future extensions in evolutionary ecology are briefly outlined. Foremost, but perhaps the most difficult among these, are ecosystem analyses.

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XVII

Enmergy* in Ecosystems

by

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Introduction

In the hierarchy of Nature, energy is transformed successively through many stages, resulting in products that are essential to ecosystems and to the economy of humanity. The solar energy required for a product of Nature is called the Solar ENMERGY (solar enmjoules). The solar enmergy required to generate a joule of each kind of product is the solar TRANSFORMITY of that product. In this chapter the enmergy concept is applied to ecosystems.

Just as the work of humans and machines generates inputs to the economy, the work processes of Nature also contribute. By evaluating Nature's work in making soils, minerals, clean water, biomass, information, etc., on the same enmergy basis as the works of humans, the dollar or other currency values of various aspects of Nature are estimated. These methods allow choices to be made as to which uses and management of Nature contribute most to the combined economy of humanity and Nature.

Review of Previous Studies

Ideas of energy being the basis of all natural and other phenomena developed with the concepts of energy in the last century. Thus Boltzmann (1905) described the struggle for existence as the struggle for free energy, while Maxwell (1877) generalized the concept of work as energy transformation. The acceptance of the Second Law of Thermodynamics implied that degraded energy was inferior, and that not all energy could do work. Carnot's formulation (1824) showed the fraction of heat that could be converted to

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* Originally called 'emergy', but *see* footnote and text on page 343.—Ed.