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Source: *Ecology*, Vol. 56, No. 5 (Late Summer, 1975), pp. 1201-1208
Published by: Ecological Society of America
Stable URL: http://www.jstor.org/stable/1936160
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Ecology (1975) **56**: pp. 1201–1208

EVOLUTION OF MARINE SYMBIOSIS—A SIMPLE COST-BENEFIT MODEL[1]

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Abstract. A simple cost-benefit analysis of symbiosis from the guest's point of view is developed for (1) the conditions under which symbiosis should form, (2) the extent to which the association should be facultative or obligatory for the guest, (3) the conditions for the evolution of mutualistic activity by the guest, and (4) the optimum amount of mutualistic activity by the guest. Some predictions are that: rare species and species with short life-spans in a taxon of potential hosts should have fewer coevolved parasites; facultative parasites on unpalatable or well-protected hosts should be more deleterious to their hosts than those on comparatively vulnerable hosts; and mutualism should only evolve in hosts of intermediate survival ability. The use of the theory is illustrated with data on the damselfish-sea-anemone associations.

Key words: Damselfish; evolution; marine biology; mutualism; parasitism.

INTRODUCTION

An intriguing phenomenon especially common in marine environments is the occurrence of pairwise symbiotic associations among species of characteristic taxa. For example, species of hermit crabs, genera *Pagurus*, *Eupagurus*, and *Dardanus* associate with species of the sea anemone genus, *Calliactis* (Cutress et al. 1970, Rose 1970, 1971). Also, as discussed later, damselfish of genera *Amphiprion* and *Premnas* associate with Indo-Pacific species of the anemone genus *Stoichactis* (Verwey 1930, Mariscal 1970*a*, 1970*b*; for general reviews see Dales 1957, Gotto 1969). The associations vary in several properties: extent to which the guest is obligately symbiotic; host specificity of a guest; territoriality among guests with respect to co-occupancy of a host; and, perhaps most interestingly, extent to which the guests actually incur hazard to obtain food for their host and thereby raise the fitness of their host.

In this paper, I develop a simple cost-benefit model for the evolution of a symbiotic association, assuming the free-living state is primitive, and for the evolution of mutualistic behavior by the guest. This model may contribute to the explanation of some of the variation mentioned above among naturally occurring symbiotic associations. Also, I examine some aspects of the co-evolution among hosts and guests.

A simple strategy model for the evolution of symbiosis may be particularly useful at this time. Several authors (Williamson 1972, May 1973) suggest, as a generalization, that mutualistic associations are rare in nature. The truth of this proposition is clearly disputable in view of the many associations involving plant roots, the ubiquity of insect mediated plant pollination, as well as many marine associations. In addition, the evolution of reduced parasite virulence is a problem similar to that of the evolution of mutualism. It is widely believed that parasites do not harm their hosts as much as they "could." Indeed the time course of the evolution of reduced virulence has been documented in myxoma virus in Australian rabbits (Fenner 1965). Nonetheless, May (1973), upon examining the criteria involved in detecting community stability from the signs of the elements of the community interaction matrix, suggests that mutualism leads to community instability and hence ought to be rare in nature. I suggest however that a logically prior issue is an examination of the conditions under which mutualism is a good strategy. For the evolution of mutualism must first be a viable strategy before the spectre of community instability should be raised.

MODEL

Initial formation of the association

It is visualized that the initial formation of an association occurs when the fitness of a symbiont strategy exceeds that of a free-living or solitary strategy. Thereafter, given an established symbiosis, the issue of possible mutualistic behavior by the guest may be raised, and this issue is treated later. The following parameters are used in the model.

Solitary strategists:

W_{ss} = fitness of an individual who has not attempted to colonize a host and is surviving as a free-living individual.

Symbiont strategists:

P = probability that an individual of the symbiont phenotype successfully finds a host,

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[1] Manuscript received 28 November 1972; accepted 18 March 1975.

L = probability that the host survives while the symbiont is associated with it,

W_a = fitness of a symbiotic individual who has successfully found a host and is associated with it, and

W_{sg} = fitness of a symbiotic individual who has failed to find a host or whose host has died.

I assume that the search for a host involves some cost, e.g., passing up suitable sites for a solitary dwelling, devoting energy for the search which would otherwise be used in nest construction, and increased exposure to predation hazard. As a result of this cost, a guest who has failed to find a host has lower fitness than one who has not tried, i.e., $W_{sg} < W_{ss}$. The cost of finding a host is defined as $C = W_{ss} - W_{sg}$. (Note that C cannot exceed W_{ss} since W_{sg} cannot be less than zero.) However, success in finding a host results in more fitness than solitary existence (otherwise, of course, there is no conceivable merit to the symbiosis), so $W_a > W_{ss}$. The benefit of the association is defined simply as $B = W_a - W_{ss}$. The question then becomes when is the cost of finding a host worth the return?

The expected fitness of the symbiont strategist is

$$PLW_a + (1 - PL)W_{sg}. \tag{1}$$

If the symbiont successfully finds a host and the host lives, then its fitness is W_a. Otherwise, the fitness is W_{sg}. Meanwhile, the fitness of the solitary strategist is simply W_{ss}. Hence, for the symbiont strategy to be more fit we require

$$\begin{aligned} PLW_a + (1 - PL)W_{sg} &> W_{ss} \\ W_a > W_{ss} &> W_{sg}. \end{aligned} \tag{2}$$

Substituting the definitions of cost and benefit

$$\begin{aligned} C &= W_{ss} - W_{sg} \\ B &= W_a - W_{ss} \end{aligned} \tag{3}$$

and rearranging yields

$$[PL/(1 - PL)]B > C. \tag{4}$$

By this formula the cost of finding a host is profitable in terms of fitness if the benefit of the associated state times the quantity $PL/(1 - PL)$ is greater than the cost. If PL is near one, i.e., if both finding a host is nearly certain and the host's survival is nearly certain, then an infinitesimal benefit is worth a large loss in ability to survive in a solitary state because then the formation of symbiosis is seen as a certainty. However, as PL becomes smaller the benefit from the association needed to justify some cost becomes increasingly large. Thus, for symbiosis to evolve, three factors must occur: (1) the host should be easy to find, (2) the host should survive well with the symbiont, and (3) the host should provide substantial benefit to the guest.

The factors which promote symbiosis are obvious, yet I think the first two are often ignored in favor of the third. Those trying to explain why parasites are associated with certain organisms and not others usually focus on the occurrence of morphological features, e.g., ciliary tracts, gastric cavities, etc., all of which would be quite beside the point if there were not reasonable assurance of the host's survival or if the host were so rare or inaccessible as to be difficult to colonize. Moreover, taking account of the first two factors leads to certain predictions. The rarer species in a taxon of potential hosts should have fewer endemic parasites. Also, the species with life histories involving short lifespans should also have fewer endemic parasites. In particular, r-selected species should have a lower parasite burden than K-selected species. (Here I distinguish host-specific parasites from host-nonspecific parasites because it is only the former who evolve to the specific properties of their host.)

Optimum host dependency

The previous consideration indicates whether a symbiotic strategy is better than a purely free-living strategy. If the symbiosis can form we might ask, how strong should the association be? Should the guest sacrifice all ability to survive in a solitary state and become obligately symbiotic (visualize larvae with an absolute requirement for the host in order to metamorphose), or should it evolve some optimum degree of facultative dependency (visualize larvae which settle on alternate substrate or hosts after a certain time)?

To answer this question, I assume the probability of finding a host, P, is an increasing function of the cost, $(W_{ss} - W_{sg})$ and find the level of cost, C_*, which maximizes the difference in fitness between the symbiont and solitary strategies. To obtain C_* explicity we must assume a particular function for $P(C)$. In addition to being monotonic increasing in C, it should have a "diminishing return" property. Initial increments of cost should contribute more to increasing P than later increments; that is, it should be increasingly hard to raise the colonization probability as the colonization probability approaches one.

Moreover the function should asymptote at 1 since P is a probability and cannot exceed 1. One function satisfying these criteria is the rectangular hyperbola, perhaps familiar to the reader from Michael-Menton chemical kinetics:

$$P(C) = C/(C'' + C) \tag{5}$$

the function is parameterized by C'', the cost necessary to produce a probability of host colonization of ½. (If $C = C''$, then P = ½.) Note a low C indicates that each unit of cost is effective in increasing the probability of finding a host, a high C'' indicates that each unit of cost is comparatively ineffective.

Of course (5) is a special assumption and it may be possible to contrive other expressions for $P(C)$ which would lead to different conclusions. However (5) is a reasonable first choice for a function having the diminishing return feature, and the conclusions are easily generalized to other functions. The expression for the difference between the fitness of the symbiont and the solitary strategy upon substituting B and C from (3), is

$$PL(B+C)-C. \qquad (6)$$

Substituting $P(C)$ from (5), differentiating with respect to C and setting equal to zero yields a quadratic for C_* whose appropriate solution is

$$C_* = C''\left[-1+\left(1+\frac{LB-C''}{C''(1-L)}\right)^{\frac{1}{2}}\right]. \qquad (7)$$

This expression indicates that the optimum host dependency increases with the benefit the host provides, B, and especially strongly with L the host survival. Of particular interest is a threshold for the evolution of the association which occurs at

$$LB = C'' \qquad (8)$$

The more difficult the host search (high C'') then the larger must be LB for any symbiosis to evolve. If LB is less than C'', the association will not form. Also, as C'' becomes larger, the optimum cost C_* drops. Note especially the dependence on L. If L is near 1 then a fully obligate association should readily evolve since C_* will be very large. By definition, if C_* is larger than W_{ss} the association is fully obligatory to the guest.

Now examine both (7) and (4) together. For the association to form by (4) the host survival, L, must be large. And by (7), if L is high then C_* is high. But, as mentioned above, $C_* > W_{ss}$ indicates an obligate association. It should be easy to obtain a $C_* > W_{ss}$ because W_{ss} is between 0 and 1, whereas C_* varies inversely with $(1-L)$. Thus it appears that parameter values satisfying (4) are also likely to produce an obligate association. If so, it is predicted that facultative endemic commensals and parasites should be significantly rarer than obligate commensals and parasites.

Evolution of mutualism

Once a symbiotic association is established, the issue arises of the possible evolution of mutualistic behavior by the guest toward the host. Such behavior might take the form of the guest catching additional food with concurrent exposure to predation hazard in order to feed (or farm) its host. The evolution of such mutualism turns on whether a guest who sacrifices some of the benefit he extracts from the host in order to improve his host's survival is fitter on the average than a guest who extracts the maximum benefit from the host regardless of the consequences to the host's survival. I now derive this condition and express it in terms of costs and benefits as before. Consider the following parameters some of which were introduced before:

L_m = probability of survival of a host who is associated with a mutualistic guest and

L_p = probability of survival of a host who is associated with a nonmutualistic (i.e., parasitic) guest.

By definition $L_m > L_p$.

W_{am} = fitness of mutualistic guest in associated state and

W_{ap} = fitness of parasitic guest in associated state.

By definition $W_{ap} > W_{am}$.

W_{sg} = fitness of a guest who has failed to find a host or whose host dies and

W_{ss} = fitness of a solitary strategist—one who does not attempt symbiosis.

The costs and benefits may be defined as:

$C \;= W_{ss} - W_{sg}$, cost of host search;
$S \;= W_{ap} - W_{am}$, sacrifice of mutualist; and
$B_{\max} = W_{ap} - W_{ss}$, maximum benefit of the symbiotic association to a guest.

Using these parameters the condition for the mutualist to be the more fit on the average is

$$PL_m W_{am} + (1-PL_m)W_{sg} > PL_p W_{ap} + (1-PL_p)W_{sg}. \qquad (9)$$

Substituting the definitions for C, $B_{\max}$, and S and rearranging gives

$$[B_{\max}+C][(L_m-L_p)/L_m] > S. \qquad (10)$$

By this formula, the sacrifice made by the mutualist to improve its host's survival is profitable in terms of his own fitness if the maximum benefit which could be provided by the association, $B_{\max}$, plus the cost of finding the host, C, times the quantity $(L_m-L_p)/L_m$ is greater than the sacrifice. Then the factors which promote mutualism are: (1) a host which provides a considerable improvement over a purely solitary existence; (2) a high dependency by the guest for the host as reflected in the loss of ability to survive in a solitary state resulting from unsuccessful host search; and (3) a mutualistic behavior which does in fact give a large improvement to the host's survival, i.e., a behavior which makes (L_m-L_p) large.

The optimum degree of mutualism

To determine the optimum degree of mutualism, I assume the improvement in the host's survival $(L_m - L_p)$ is a monotonic increasing function of the sacrifice made by the guest on the host's behalf. Again, a diminishing return property is necessary, as is an asymptote at $(1 - L_p)$ which is the maximum possible improvement. To obtain an explicit solution, I assume the rectangular hyperbola as the function relating the improvement in the host's survival to the guest's sacrifice

$$[(1 - L_p)S]/[S'' + S]. \qquad (11)$$

Here S'' is the value of the sacrifice which produces one half the maximum possible improvement in the host's survival. Then forming the expression for the difference in fitness between the mutualist and nonmutualist, substituting for $B_{\max}$, C and S: and for L_m from (11) gives

$$P\{[(1 - L_p)S]/[S'' + S] + L_p\} \cdot (B_{\max} + C - S) - PL_p(B_{\max} + C). \qquad (12)$$

Differentiating (12) with respect to S, and setting equal to zero yields a quadratic whose appropriate solution is

$$S_* = S''\left[-1 + \left(1 + \frac{B_{\max} + C - S''L_p/(1 - L_p)}{S''[1 + L_p/(1 - L_p)]}\right)^{\frac{1}{2}}\right] \qquad (13)$$

S_* from (13) is the optimum sacrifice a guest should make to improve his host's sacrifice. When S_* is below zero, the nonmutualist is favored and when S_* equals zero, the two strategies are equally fit. S_* equals zero marks a threshold which occurs at

$$B_{\max} + C = S''L_p/(1 - L_p). \qquad (14)$$

When $B_{\max} + C$ is greater than $S''\ L_p/(1 - L_p)$ then mutualism can evolve, but below this threshold full exploitation prevails. Above the threshold, S_* increases approximately as $\sqrt{B_{\max} + C}$. The property that the slope of S'' becomes continually less steep follows from the diminishing returns feature of the assumed relation (11) between the improvement in the host's survival and the guest's sacrifice.

The formula for the threshold (14) indicates a high threshold if L_p is near one. Hence, if the host already survives well, the benefit obtained from the host and the fitness expended in the host search must both be high for mutualism to evolve. This result merely restates the earlier point that, for mutualism to evolve, the host must originally survive poorly enough so that an improvement can in fact be achieved. One might expect to find then that the commensals on unpalatable or well-protected hosts should be more deleterious to their hosts than those on comparatively vulnerable hosts.

TABLE 1. Example of the evolution of symbiosis. Calculations assume $C = 0.3$, $P = 0.9$, $B_{\max} = 0.5$, $S = 0.25$, and $L_m = ½\ (1 - L_p) + L_p$

Host	Host's survival (L_p)	Will an association form? condition (4)	Will mutualism evolve? condition (10)	Net result
No. 1	0.3	−	+	No association
No. 2	0.5	+	+	Mutualism
No. 3	0.7	+	−	Parasitism
No. 4	0.9	+	−	Parasitism

Joint evolution of host dependency and mutualism

Thus far the issue of initial formation of the symbiosis together with the concomitant evolution of host dependency has been treated as a separate issue from the evolution of mutualism. Yet synthesizing the theory on those issues leads to some additional results.

First, by condition (10) mutualism will evolve only if the host survives poorly enough so that an improvement is actually feasible, while by condition (4) the association cannot form unless the host's survival is high. Therefore we should observe mutualism only on hosts of intermediate survival ability; those with lower ability will not have any association at all, while those with higher ability will have guests who cannot justify incurring hazard to improve their host's survival even more. For example, consider a set of four potential hosts whose probabilities of survival during the guest's life span, L_p, are 0.3, 0.5, 0.7, and 0.9 (Table 1). Then suppose the cost of finding a host, C, is 0.3, and the resulting probability of finding a host, P, is 0.9; and also that the benefit of being associated, $B_{\max}$ is 0.5, then the host whose L_p is 0.3 does not satisfy condition (4) and will not evolve an association while the others will. Now suppose in addition there is a possibility for the guests to sacrifice their fitness in the amount $S = 0.25$ to improve the host's survival by one half the amount by which L_p differs from 1, so $L_m = ½\ (1 - L_p) + L_p$. Then this form of mutualism will evolve in the host whose L_p is 0.5 but not in the others. So the sequence of evolutionary results in the hosts are respectively: no association, mutualism, parasitism, parsitism.

I have been assuming that the evolutionary path to mutualism passes through a parasitic phase. This assumption is self-consistent in the sense that, if condition (4) is initially satisfied, then evolution of

TABLE 2. Damselfish-sea anemone associations in Batavia Bay (summary of Verwey [1930])

Fish genera—*Amphiprion* and *Premnas*		Anemone—genus *Stoichactis*	
Remarks	Name	Name	Remarks
1) Inhabits anemones 1 & 4 without preference 2) Must leave anemone 1 when exposed at low tide 3) Does not bring food to anemone 4) No "host care" behavior 5) Least territorial and co-occupancy of anemones 6) Most abundant anemone fish 7) Many broods (> 3/yr)	*A. percula* 8 cm	#1	1) Lives only in shallow water, often in lagoons 2) Silt tolerant 3) Often exposed at low tide
1) Inhabits anemone 4 2) Rare in Batavia Bay 3) Never observed bringing food to host	*A. akallopisus* 9.5 cm	#4	1) Grows on coral rock and on coral fragment bottom in full sunlight 2) Individuals cluster giving appearance of a carpet
1) Inhabits anemones 2 & 3 but prefers 2 when available 2) Rare in Batavia Bay 3) Brings large food items to feed its anemone host 4) Eats small food items itself	*A. polymnus* 13.6 cm	#2	1) Rare in Batavia Bay 2) Requires clear water, usually found below 3 m 3) Grows between and on corals and coral rock, never in sandy places
1) Adults prefer anemone 5 over anemone 3 2) Young usually found in anemone 3, either by preference or having been forced there by adults 3) Brings food to anemone host 4) Three broods/year	*A. ephippium* 12 cm	#3	1) Preference for open sandy places between large *Porites* colonies and *Acropora* thickets 2) Often abundant 3) Inhabits clear and muddy waters
1) Only found in anemone 5 2) Brings food to anemone host 3) "Host care" behavior 4) Deepens holes for anemone 5 to attach in 5) Strongly territorial; when pursued, attacks and bites intruder 6) Three broods/year	*Premnas biaculeatus* 16 cm	#5	1) Inhabits deep crevices and holes between and in large colonies of *Porites*, *Maeandra*, and others 2) Requires dim light

Important facts about all fish

1) All receive predation protection; when any of the damselfish are placed in an aquarium with small groupers or snappers, they are immediately eaten unless an anemone is also in the aquarium.
2) All occasionally feed directly on the anemone's tentacles and scavenge food from the region of the anemone's oral disc.
3) None of the fish are ever found without an anemone.

any mutualism by (10) cannot cause (4) to be violated. This is true because if (4) is satisfied the parasitic phase is fitter than the solitary phase, and if (10) is satisfied then the mutualist is fitter than the parasite so the mutalist is also necessarily fitter than the solitary phase. This path would seem the most reasonable evolutionary route. However, it is possible to specify values to the parameters above such that (10) is satisfied while (4) is not for the parasite but is for the mutualist. Such an association would have to be mutualistic at its evolutionary origin and hence this path seems unlikely.

Second, with fixed host properties, the evolution of mutualism should cause the evolution of more host dependency by the guest which in turn should cause even more evolution of mutualism—the two factors reinforce each other even without host-guest coevolution. To obtain this result, observe in (7) that C_*, the optimum loss of solitary fitness due to the host search should increase strongly with L the host's survival so the effect of mutualism should increase C_*. Next observe in (13) that, S_*, the optimum sacrifice to improve the host's survival increases with C, so that an increase in the host dependency in turn produces an increase in the optimum amount of mutualism. Of course, this reciprocal reinforcement does not continue indefinitely since there is a diminishing return in both $P(C)$ and $L_m\ (S)$. The joint equilibrium can be found by writing the mutualist fitness as a function of two variables, S and C, and finding the maximum point. This leads to two simultaneous quadratics whose solution is unnecessary to the qualitative conclusion that the evolution of mutualism should lead to an association which is obligatory for the guest.

DISCUSSION

The damselfish-sea anemone associations

To illustrate the use of the cost-benefit model in explaining qualitative features of symbiotic associations I will consider in as much detail as available the damselfish-sea anemone association. Verwey (1930) studied the associations between five species of damselfish (*Pomicentridae*) and five species of of large sea anemones from the genus *Stoichactis*. The associations were all sympatric in Batavia Bay in Indonesia, although two of the fish species were too rare to obtain sufficient data. His study consisted both of underwater field observation and aquarium observation throughout several years. Verwey's study remains exceptional in that he documents not only differences among the association but also among the environmental conditions in which the associations are located (Table 2).

Focus attention on the three fish not reported as rare, *Amphiprion percula*, *Amphiprion ephippium*, and *Premnas biaculeatus*. These three form a spectrum in several characteristics. *Amphiprion percula* is a parasite—it receives several forms of benefit from the host (Table 2) and shows no mutualistic behavior. It is also in the poorest host—it must leave at low tide. As a result, it presumably incurs more predator hazard and must expend more effort reacclimating an anemone to its presence. Also, *A. percula* has the least host specificity, is the least territorial, the most abundant, the smallest in size, and has the highest reproductive commitment. *Amphiprion ephippium* is a moderate mutualist since it feeds its host. It also has moderate host specificity, moderate territoriality, moderate abundance, moderate size, and with only three broods a year, it has a lower reproductive commitment than *A. percula*. (The first brood of the season begins in late March to early April and is tended by the males who are generally smaller than the females.) *Premnas* is the extremist. It has several mutualistic activities: host feeding, preparation of suitable crevices and holes for its long stalked host, and a curious "host care" behavior which is reported to revive the anemone if it is physiologically stressed as in transporting the anemone from the ocean to an aquarium containing the fish. Also, *Premnas* has the most host specificity and the most territorially related aggressiveness. It has three broods per year and apparently is moderately abundant. All these characteristics of the three fish species should be predicted by assessing the characteristics of their hosts in light of the cost-benefit model.

The anemones show niche separation with respect to microhabitat preferences as shown in Table 2. Let us concentrate on anemones Nos. 1, 3, and 5 as these are principally involved in the symbiosis. Number 1 is exposed at low tide, forcing its guests periodically to leave its protection. This anemone clearly confers the lowest possible benefit, $B_{\max}$. Hence, guests of this anemone should evolve the least mutualism by (13) and the least host dependency by (7). And indeed, *A. percula* is the parasite and shows the least host specificity. Moreover, *A. percula* should be the least able to afford the luxury of territorial disputes especially for an anemone which must be regularly vacated. But due to the lack of territoriality co-occupancy of anemones occurs and hence a higher population size assuming anemones, and not food alone, are limiting. That *A. percula* indeed receives the least protection and the highest mortality is supported by the life history characteristic of a high reproductive commitment. It is the *r*-strategist of the three fish. The apparent paradox between asserting that anemone No. 1 is the worst host and the fact that *A. percula* is the most abundant fish is attributed, I think, to the lack of territoriality.

Had not the apriori cost-benefit model been developed, this paradox involving the abundance of *A. percula* would have prevented any attempt to explain the lack of mutualism in *A. percula* in terms of Anemone 1 being a poor host.

Anemones No. 3 and No. 5 are always submerged and should provide about the same benefit $B_{\max}$ to a guest. But No. 5 is rarer than No. 3 because of its restrictive microhabitat preferences. Hence any guest of No. 5 must differ from that of No. 3 by incurring a higher cost of host search. In terms of the model, a guest of No. 5 has a higher C'' than that of No. 3 and by (7) should evolve a higher dependence for that host. Also, a guest of No. 5 should be able to perform new categories of behavior to help the host in its special microhabitat, e.g., the substrate preparation by *Premnas*. Any such new kinds of behavior reinforce the fish's dependence on the host. Higher host dependency in turn leads to more mutualism by (13). Thus the guests of No. 3 and No. 5 should differ principally in the degree of mutualism and host specificity but not in characteristics related to $B_{\max}$. Indeed, *A. ephippium* and *Premnas* do differ in these ways while they have the same reproductive commitment—consistent with assuming their mortality protection, $B_{\max}$ is about the same. As an incidental consequence of the common high $B_{\max}$, both are territorial and their population sizes reduced as a result. The increased aggressiveness of *Premnas* is expected in view of its commitment to anemone No. 5 and the willingness to *A. ephippium* to occupy this same host when available. Again, the model has been important in this interpretation. Without it we would not have been led to attribute significance to the microhabitat preferences of anemone No. 5. Because of its restriction to special microhabitats it is argued that a guest of No. 5 must be more host specific and mutualistic than a guest of more cosmopolitan anemones.

This account is in principle testable in many ways. The key points to the account are that anemone No. 1 differs from No. 3 and No. 5 in $B_{\max}$, while No. 3 differs from No. 5 in searching cost and in the variety of ways assistance is possible. For example, if another population of *A. percula* somewhere else is associated with a fully submerged anemone, then it should be mutualistic there; if a population of anemone No. 1 is fully submerged somewhere else its symbionts should be mutualists; or if a population of anemone No. 1 is also exposed at low tide somewhere else then its guest should not be mutualistic, etc. Similarly if *Premnas* is associated with a more common and cosmopolitan anemone somewhere else it should not be as mutualistic and specific as it is toward anemone No. 5. In short, a good qualitative test will come from the analysis of biogeographic patterns in the symbiotic associations.

The cost-benefit model yields an equilibrium theory. It differs fundamentally from a nonequilibrium account which, for example, would attribute each species of fish to an evolutionary grade.

Some issues in host-guest co-evolution

The discussion thus far has been solely concerned with characteristics of the guest but obviously the host population evolves too. The host has the evolutionary option of attempting to promote or repulse colonization by guests. Clearly the host should encourage colonization if the guest improves its fitness and discourage it otherwise (e.g., see the *Oropendola*—cowbird study of Smith 1968). But the evolution of mutualism on the part of the guest cannot be based on expectation of reciprocation in future generations by the host but instead is always adjusted to the current properties of the host. (For the population genetic theory of density-dependent coevolution among several species see Roughgarden 1976.) As a result three cases can occur: (1) the host may be such that no sacrifice on the guest's part is justified ($S_* = 0$), (2) some mutualism may be justified ($S_* > 0$) but not enough to fully compensate for the exploitation by the guest (i.e., L_m is less than the host's survival without any guest at all), or (3) enough mutualism may be justified (S_* large enough) that the host is actually better off with a guest than without. In the first case, the guest is a pure parasite, in the second it is what I term a "gentle parasite," and in the third case a true reciprocally mutualistic association can develop. In many situations, it may seem to observers that the ideal strategy would be a fully mutualistic association. But this cannot evolve unless the optimum guest sacrifice, S_*, happens to lead to a net improvement in the host's fitness. But often the optimum guest sacrifice will simply reduce the virulence of the guest but not lead to a net improvement for the host.

To summarize, a simple cost-benefit model for the evolution of symbiosis has been presented which has proved useful in several respects. First, the model allowed the derivation of many predictions about the properties of a guest species given properties of the host. Second, the model led to a non-obvious hypothesis for the differences among the symbiotic associations of damselfish and sea anemones in Batavia Bay, Indonesia. Third the model allows us to assess in general terms whether reciprocal mutualism can "easily" evolve by natural selection in two species. In Table 1, it is seen the conditions for mutualism to evolve are restrictive, one requirement being that the host survive neither too well nor too poorly but have instead an intermediate survivorship. Moreover, Table 1 lumps together the evolution of reduced parasite virulence with that of time reciprocal mutualism. But true mutualism requires not merely an optimum guest sacrifice, S_*, to be greater than zero, but to be large enough that the host survives better with a guest than without. This requirement compounds the restrictiveness illustrated in Table 1. In view of these restrictive conditions it is surprising that mutualism is as common as it appears to be.

ACKNOWLEDGMENTS

I thank Drs. J. Hickman, R. Holm, S. Levin, C. Sassaman, A. Schoener, and T. Schoener for helpful suggestions on the manuscript.

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