

Money-in-the-bank: a model for coral reef fish coexistence*

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Synopsis

An alternative to the 'reef fish lottery' model is proposed for explaining instances of coexistence of reef fishes without apparent spatial resource partitioning. This model is termed 'money-in-the-bank' because of a financial analogy used to explain it. It stresses the importance of habitats that can support only one of two or more closely related species that coexist elsewhere. Populations living in such monospecific habitats could, according to the model, produce enough larvae to repopulate these habitats plus an excess that may settle in the multispecific habitats. Possible examples among cardinalfishes are given.

Introduction

According to the space resource sharing hypothesis of Smith & Tyler (1972, 1973) the fineness of spatial resource subdivision is the basis of the numerical stability of highly diverse coral reef fish communities. This view is consistent with the competitive exclusion principle and provides an important perspective for understanding many of the adaptations of reef species.

Sale (1974, 1975) has shown that some instances of reef fish coexistence do not conform to this orderly explanation, particularly among species of the territorial pomacentrid guild that inhabit rubble patches. These species coexist even though space is apparently limiting and the fish apparently have identical space requirements. Moreover, there is no ten-

dency for a patch to revert to its original species composition after experimental disruption as might occur if the species composition resulted from a systematic partitioning of living space. Sale & Dybdahl (1975) studied small-scale species distribution patterns in simple habitat units, but failed to find any seasonal partitioning of space, subtle microhabitat specializations, or evidence of mutual exclusion from such units.

These findings led Sale (1974, 1975, 1976) and Sale & Dybdahl (1975) to propose an explanation of reef fish coexistence that emphasizes stochastic factors rather than orderly resource partitioning. In this view chance colonization and chance mortality determine small-scale distribution of species and promote coexistence. The overall mechanism may be viewed as a reef fish lottery (Sale 1974, 1976, these proceedings) in which superabundant pelagic larvae are tickets in a lottery for space on the reef — a lottery won by first arrivals. Coexistence continues because no species wins or loses all the time.

This model has provided a valuable new perspective for understanding reef fish ecology. Certain considerations, however, may argue against its general applicability. If the population of reef fish larvae may be viewed as a multispecific pool drifting over fairly wide geographic areas, then random recruitment from this pool would reflect the relative proportions of the different larval species in the pool. Within this framework, either each species somehow always has the average larval population (average in spatial and temporal terms) necessary to continually renew its proportion of the adult population, or one species will, based on the slightest competitive advantage, tend to progressively enhance its proportions in the larval pool and thus in the adult population, eventually ex-

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cluding the other species. In terms of the lottery analogy, if one species can buy at least a few more tickets than another for each drawing, then that species' statistically inevitable greater number of wins will, by positive feedback, eventually eliminate the other species from the game.

Avoidance of this elimination would require some counterbalancing mechanism or negative feedback control. Sale (1974) cites Beverton & Holt (1957) in support of one possibility, that high mortality of pelagic larvae has some homeostatic effect on relative recruitment proportions, but how this would work is not explained. One possibility would be preferential predation on the more abundant larval species. That larvae of closely related species might differ enough for such predator selectivity is supported by McPhail's (1969) demonstration that larvae of two genetic varieties of stickleback show behavioral differences affecting their vulnerability to predation.

Money-in-the-bank model

In the alternative model (and financial analogy) presented below, two or more species ('investors') can coexist in some habitats ('stock market') because of excess larva production ('interest') in other habitats ('savings banks') in which they occur alone.

Analogy

At yearly intervals, investors *a*, *b*, and *c* convert all their investments into cash, which they then reinvest. At each reinvestment time investors *a*, *b*, and *c* put \$ 10,000 into 5% annual interest accounts at savings banks *A*, *B*, and *C*, respectively, and a variable amount in the stock market (*X*). A year later each investor converts his bank account (\$ 10,500) and stocks into cash. He then reinvests \$ 10,000 in the bank and the remainder in the stock market. Each year he plays the stock market with an amount equivalent to the money obtained from selling last year's stocks plus his bank interest. No matter how badly his stocks do in any year, he always has at least \$ 500 to invest in stocks the next year. The continued presence year after year in a fluctuating stock market of investors *a*, *b*, and *c*, whose luck and investment wisdom may noticeably differ, will puzzle the observer who is unaware of the bank accounts, and who looks only where all three investors are found together, i.e., the stock market.

Model

In the model, investors *a*, *b*, and *c* represent three sympatric reef fish species. Institutions *A*, *B*, and *C* are habitats into which only species *a*, *b*, and *c*, respectively, can recruit successfully and grow to maturity. *X* is a habitat type that can and often does support all three species. Luck and investment wisdom are analogous to chance and competitive advantage. *X* habitats may be more common; consequently we would tend to conclude that the co-occurring species have very similar habitat preferences. It is the diversity observed in *X* habitats that we usually try to explain.

Assumptions

This system could maintain a dynamic equilibrium if: 1. the planktonic larvae of these three species constitute a 'pool' within which at least some of the larvae disperse over wide geographic areas, 2. the species in question are sedentary after recruitment, and 3. adults of a species living in its monospecific habitat produce enough larvae to insure repopulation of that habitat, plus a sufficient excess to enter into competition with other species in the multispecific habitats.

Assumptions 1 and 2 are more or less similar to assumptions made by Sale (1974, 1976) for the reef fish lottery model, and probably apply to a wide variety of reef fish species. Assumption 3 is an extension of assumption 1.

Features

I. The relative success of *a*, *b*, and *c* in repopulating *X* habitats could be variable, depending on chance and differences in competitive advantage in *X* habitats. If the *a*-*A*, *b*-*B*, and *c*-*C* relationships did not exist and only *X* was available to *a*, *b*, and *c*, these two factors would promote competitive exclusion. The model allows a large stochastic element to operate in *X* habitats without upsetting the dynamic equilibrium.

II. *A*, *B*, and *C* could be rare habitats if a great excess of larva production is assumed, or less rare if less excess is assumed.

III. There are two possible relationships between *a* and *A*, etc.:

1) *A* is a marginal habitat for *a*, *b*, and *c*, all of which settle there, but only *a* survives.

2) *A* is the 'preferred' habitat of *a*, and selection has promoted its tendency to recruit there; *b* and *c* do not recruit there successfully.

Natural selection would tend to drive condition 1) to condition 2), leading to greater and greater differences in habitat preference, and less and less coexistence. Ultimately *a*, *b*, and *c* would not be competitors; selection could lead to adaptation and a decrease in what Slobodkin & Fishelson (1974) have termed 'point diversity'.

IV. If we look at the species in question only in *X* habitats (where we would tend to concentrate our observation, in an effort to understand that diversity), the apparent identity of their habitat requirements would seem to be the proximate factor resulting in coexistence of the three species. This coexistence ultimately depends, however, on the niche differences operating in *A*, *B*, and *C* habitats — differences we would not tend to see in *X*. Thus habitat similarity is required for the coexistence to be observable at a point in space and time, but would promote competitive exclusion in the long run, in the absence of *A*, *B*, and *C* habitats.

V. Production of superabundant larvae over a prolonged breeding season seems to be a characteristic that has evolved in many reef fish families, and this characteristic would allow the great diversity we observe in these groups. In fact, excess recruitable larva production would be selected for in this model.

VI. The larval pool would act as a buffer, insuring that local extinctions are only temporary, since such extinctions would have little effect on the number of recruits available to repopulate that area.

VII. In a variant of the model, two species could coexist in *X* habitats even if only one had a bank account habitat, as long as the other species had a decisive competitive advantage in *X* habitats.

VIII. *A*, *B*, and *C* habitats could take several different forms:

- 1) a suboptimal microhabitat — perhaps some facultative symbioses serve this purpose,
- 2) a marginal, broad habitat type or depth range,
- 3) a geographic refugium, e.g., if the upcurrent edge of the range of species *a* is beyond that of *b* (perhaps *a* can tolerate some environmental extreme better than *b*) then this fringe area would be the *A* habitat or bank account of species *a*.

Examples

In the course of studying the comparative ecology of cardinalfishes (family Apogonidae) in the Bahamas

(Dale 1975, 1978), I have analyzed 125 rotenone collections which included one or more apogonid species and have obtained certain patterns which seem to fit the money-in-the-bank model.

For example, in terms of a classification of broad habitat types (C. L. Smith, unpubl.), *Apogon lachneri* is absent from the rocky shoreline habitat but common at the dropoff, while *A. maculatus* is absent at the dropoff and common at rocky shorelines. In a third habitat type, outer shelf patch reefs, both species are present, often in the same sample. This habitat tends to have the greatest apogonid species richness (as well as the highest overall fish diversity) of the three. These data are summarized in Table 1. The

Table 1. Frequency of occurrence (F) and total specimens (S) of two *Apogon* species in rotenone collections from selected broad habitat categories in the Bahamas. The number of collections from each habitat is shown in parenthesis. Also shown for each habitat category is the mean apogonid species richness, i.e., the mean number of apogonid species per collection.

	Rocky shoreline (22)		Dropoff (12)		Outer shelf patch reef (35)	
	F	S	F	S	F	S
<i>Apogon lachneri</i>	0	0	0.833	89	0.200	13
<i>Apogon maculatus</i>	0.773	95	0	0	0.829	373
Mean apogonid species richness	2.95		3.00		3.54	

Table 2. Frequency of occurrence (F) and total specimens (S) of two *Apogon* species and two *Phaeoptyx* species in rotenone collections made at three depth ranges in the Bahamas.

	0–3 m (43)		9.5–12 m (16)		28–43 m (9)	
	F	S	F	S	F	S
<i>Apogon phenax</i>	0	0	0.313	13	0.333	4
<i>Apogon binotatus</i>	0.256	88	0.313	22	0	0
<i>Phaeoptyx pigmentaria</i>	0.465	51	0.563	23	0.222	2
<i>Phaeoptyx xenus</i>	0.023	1	0.188	4	0.333	7

money-in-the-bank interpretation would be that the rocky shoreline and the dropoff are the *A* and *B* habitats of *A. maculatus* (*a*) and *A. lachneri* (*b*), respectively, and that the outer shelf patch reef is the *X* habitat.

Another pair of species may serve to exemplify the model in terms of depth. In the 0–3 m range *A. phenax* is absent from all samples, while *A. binotatus* is present. In the 28–43 m range *A. binotatus* is absent and *A. phenax* is fairly common. At the intermediate depth range of 9.5–12 m both species occur, sometimes together. An additional, similar, depth example is provided by *Phaeoptyx pigmentaria* and *P. xenus* (although *P. xenus* is an obligate sponge dweller during the day, it is quite possibly a competitor of *P. pigmentaria* at night). In shallow water *P. pigmentaria* is common and *P. xenus* is rare; in deep water *P. xenus* is the more common of the two. Again, at an intermediate depth both occur, sometimes in the same sample. The depth data are summarized in Table 2. The interpretation here is that shallow water or deep water may provide bank account habitats for species that coexist at intermediate depths.

Certain examples of facultative symbioses among western Atlantic cardinalfishes might also be interpreted in terms of the model. *Apogon quadrisquamatus* and *A. aurolineatus* are each found in a variety of habitats, but both have been reported to associate in some cases with two sea anemone species (Colin & Heiser 1973), an association which may function as a bank account. The facultative associations of several different apogonid species with the long spine sea urchin *Diadema antillarum* might also represent bank accounts vis-à-vis other species lacking this habit.

The examples given above are not offered as any kind of definitive demonstration of the model, which would require far more extensive evidence.

Discussion and concluding remarks

The money-in-the-bank model may be summarized as follows. Two or more species among which there is no apparent spatial resource partitioning in the habitats in which they coexist avoid competitive exclusion because of other habitats in which they occur alone. Excess larva production from the monospecific habitats insures a continual supply of recruits for the multispecific habitats.

This model deals with the concept of niche overlap, and the variant (feature VII, see above) is a

variety of niche inclusion (see Pianka 1974, and Colwell & Fuentes 1975 for discussions of these). In either case, in the present application, the tendency toward competitive exclusion in the overlapping region is alleviated by dispersal from the non-overlapping region(s). Levin (1976a, b) emphasizes the importance of dispersal and of fugitive strategies in facilitating a similar kind of coexistence of competitors. The reef fish larval pool represents the 'bath' of his calculations.

An underlying assumption of the model is that larvae of the species in question are ecologically identical. It is possible, however, that one or more mechanisms operating at this stage provide the negative feedback necessary to prevent competitive exclusion. As mentioned earlier, differential predation on the larval species might have this function. Various other kinds of niche separation in the pelagic stage or at settling might also override the effects of postlarval competition. In the virtual absence of information on the ecology of reef fish larvae, one can only speculate on these matters.

Another somewhat tenuous underlying assumption concerns the applicability of the competitive exclusion principle. In instances where predation keeps competing prey populations below carrying capacity, the principle may not apply, as has been shown in numerous field studies (Connell 1961) and laboratory studies (Slobodkin 1964), as well as theoretically (Parrish & Sella 1970) and by simulation (Cramer & May 1972). This effect may well be relevant in the present context. Alternatively, a network of interference competition among similar species may allow coexistence without any heavy predation (Jackson & Buss 1975).

With or without these cautionary considerations I do not propose the money-in-the-bank model as a comprehensive explanation of reef fish coexistence and diversity. It may, however, help explain some apparent exceptions to the space sharing hypothesis. Perhaps other apparent exceptions will prove, upon closer inspection, not to be exceptions. On the other hand, in many cases the mechanics of short-term species distribution patterns may be best understood in purely stochastic terms.

Even communities that are stable over long periods may have a largely stochastic basis. I would suggest that the 'urn and ball game' (Cohen 1976, May 1976) is an apt metaphor for explaining some of the apparent order and determinism of larger reef fish communities. In this game an urn initially contains one black and one white ball, and then one ball is

randomly removed at a time and put back with another of the same color. After a large number of turns the proportion of white balls will tend to converge on some steady, limiting value. This value, however, is equally likely to be anywhere between 0 and 1, and essentially depends on the vagaries of the first few turns. If only one run of the game is witnessed, there is a strong illusion of determinism, even though the result depends on a purely stochastic process. In the coral reef context, the long term stability of the total biotic community of a reef may ultimately depend on the statistical accidents of early colonization. Russell et al. (1974) demonstrated the importance of chance factors in the colonization of artificial reefs by coral reef fishes.

It is unlikely that coexistence of species in the coral reef fish community, among the most diverse and complex of vertebrate communities, will be completely explainable by any one general model. As pointed out by Clarke (1977), different mechanisms may even operate among different species within a single genus. It is possible, however, that several simple, interacting mechanisms may adequately account for the greater part of the coexistence and diversity in this community. The money-in-the-bank model is here proposed as one of these mechanisms.

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Questions and answers

Kaufman: I have been doing an experiment for the past 18 months that might test your model. It looks like concrete block reefs and rubble piles of rock are your *X* habitats and that large patches of major

framework-building corals are your *A*, *B*, and *C* habitats. This is in shallow water in the Caribbean, looking at pomacentrids, acanthurids, and scarids.

McKaye: Essentially what you are saying is that Sale, Talbot, Russell et al. are looking at *X* type habitat, and Smith and Tyler are looking at *A*, *B*, and *C* — is it not?

Dale: The point is that Sale has found exceptions to the complete carving up of space and these are explained by his lottery model, but I do not think his model provides a means of escaping competitive exclusion.

Berg: Is your model falsifiable?

Dale: I am not sure, but there are other models that are not falsifiable either, so that may not be the most serious objection (laughter). Tentatively, I think it would be falsified as a general model by the demonstration of a pair of space limited species with identical ranges of habitat and microhabitat (and no seasonal or circadian differences in occupation of these), the same depth limitations, and complete sympatry. Unfortunately, that borders on a falsifying condition for competitive exclusion, which, being tautological, is not falsifiable.

Sale: (1) I find Dale's hypothesis quite acceptable. However, I doubt that it operates very often when *X* habitats are very common and *A*, *B*, and *C* habitats are all rare. This would require species *a* to be so well adapted to *A* that it produced enormous numbers of larvae which kept settling in *X* habitats. Why would the larvae do this?

(2) Also, I feel that Dale's hypothesis is more complex than mine — more complex not because there are data to be accounted for, but in order to keep the competitive exclusion faith. I think that patch theory forms a sufficient basis from which to argue. We should favor simpler hypotheses until they are proven inadequate.

Dale: (1) As I suggested in 'feature III,' the logical result of natural selection would be that the more species *a* becomes adapted to habitat *A*, the less likely its settling in *X* habitats becomes. Thus the money-in-the-bank relationship is not static but evolving — in a way that eventually brings about its own demise.

(2) I agree that simpler hypotheses are preferable, but in my view it requires more complexity to contradict competitive exclusion than to conform to it. A glance at the literature of 'patch theory' corroborates that view. The greater simplicity of con-

forming to competitive exclusion is analogous to that of conforming to another (also tautological) biological principle: natural selection. Other things being equal, a simpler explanation is needed to hypothesize that a certain structure, behavior, or whatever, is adaptive than to hypothesize that it is non-adaptive. Of course, no verification of my hypothesis accrues from either its simplicity or its conformity to competitive exclusion.

Johannes: Is there enough information available to pinpoint central and marginal habitats for Sale's pomacentrids the way Dale has done for his apogonids?

Sale: With specific reference to my three pomacentrids, I have not been able to find habitats in which only one of *Plectroglyphidodon lacrymatus* or *Eupomacentrus apicalis* occurs.

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