

CLUTCH-SIZE BEHAVIOR AND COEXISTENCE IN EPHEMERAL-PATCH COMPETITION MODELS

STEPHEN B. HEARD* AND LYNNE C. REMER†

Department of Biological Sciences, University of Iowa, Iowa City, Iowa 52242

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Abstract.—Systems of patchy, ephemeral resources often support surprisingly diverse assemblages of consumer insects. Aggregation of consumer individuals over the landscape of patches has been suggested as one mechanism that can stabilize competition among consumer species. One mechanism for larval aggregation is the laying of eggs in clutches by females traveling among patches to distribute their total fecundity. We use simulation models to explore the consequences, for coexistence of competitors, of larval aggregation that arises from clutch laying. Contrary to some previous treatments, we find that clutch laying can be strongly stabilizing and under certain conditions can be sufficient to allow competitors to coexist stably. We extend these models by considering clutch size as a variable that responds to the abundance of resource patches. Such a relationship might be expected because females should lay their eggs in fewer but larger clutches when the cost of travel among patches is high (because patches are rare). When females adjust clutch size in response to resource abundance, coexistence can be easiest when resource patches are scarce and most difficult when resources are abundant.

Many insects and other mobile consumers exploit resources that occur as numerous small, discrete, and more or less ephemeral patches, such as fungi, fruit, dung, carrion, or host plants. Although any one patch typically supports only a single generation of consumers and local competition can be intense, patchy systems often support surprisingly diverse and apparently stable assemblages of species (Elton 1966; Beaver 1979*b*; Atkinson and Shorrocks 1981). The frequent existence of strong local competition (e.g., Grimaldi and Jaenike 1984; Kneidel 1985; Hanski 1990; Blossey 1995) suggests that in many cases resource partitioning is insufficient to explain high diversity, and so other mechanisms have been sought that might foster the coexistence of competitors in patchy, ephemeral systems.

Many studies have focused on spatial pattern in these systems—in particular on the aggregated distributions of consumer individuals among patches (e.g., Atkinson and Shorrocks 1981; Hanski 1981; Ives 1988*a*, 1988*b*; Kuno 1988; Shorrocks 1990; Marino 1991; Sevenster 1996). In some theoretical models (Atkinson and Shorrocks 1981; Hanski 1981; Ives and May 1985), aggregation can allow extended coexistence of competitors without resource partitioning,

* Author for correspondence; E-mail: stephen-heard@uiowa.edu.

† E-mail: lynne-remer@uiowa.edu.

and consumers are often strongly aggregated in nature (Atkinson and Shorrocks 1984; Kneidel 1985; Wellings 1987; Ståhls et al. 1989; Rosewell et al. 1990; Jaenike and James 1991; Kouki and Hanski 1995; Sevenster and van Alphen 1996). However, the mechanisms by which this aggregation is achieved, and the consequences for competition and coexistence of aggregation produced by different mechanisms, have been controversial. Some authors (Atkinson and Shorrocks 1981, 1984; Shorrocks and Rosewell 1988) have suggested that the laying of eggs in clutches by ovipositing females could lead to stable coexistence, while others (Green 1986, 1988; Ives 1991; Sevenster 1996) have disagreed. The controversy has certainly been aggravated by the fact that most models (Atkinson and Shorrocks 1981, 1984; Ives and May 1985; Prinkkilä and Hanski 1995) have directly imposed aggregated distributions of larvae using negative binomial or other contagious distributions, rather than explicitly considering oviposition (or other sources of aggregation). Because we should not expect all forms of aggregation to have the same effects, it is crucial that we explore more realistic models—models that incorporate the mechanisms underlying the distribution of consumers in patchy systems (Kretzschmar and Adler 1993).

We have reexamined the role of clutch laying in generating aggregated distributions of consumers on patchy and ephemeral resources and the effects of this aggregation on competition and the coexistence of competitors. We have also stepped back a little further to consider what might influence clutch-size decisions by ovipositing females. In particular, we consider the implications for competition and coexistence of female behavior that adjusts clutch size in response to changing costs of search for, and travel among, resource patches (Iwasa et al. 1984; Parker and Courtney 1984; Skinner 1985; Mangel 1987; Heard 1998). In this context, clutch-size decisions are closely analogous to optimal foraging decisions. A female laying a few large clutches incurs a relatively high cost of sib competition among her offspring (e.g., Mitchell 1990), but a female laying many small clutches incurs high search and travel costs. An optimum clutch-size strategy balances these competing costs, and a female behaving optimally will adjust clutch size as search and travel costs change. Notably, we would expect search and travel costs, and therefore clutch sizes, to increase as resource patches become rare and so more difficult to find and visit (Heard 1998).

Our models deal with the coexistence of two competitors in a system of ephemeral resource patches. We focus on the common case in which relatively immobile larvae are distributed over resource patches by adult females; therefore, we ignore the possibility of dispersal by larvae. We are interested in whether aggregation due to clutch laying can produce stable coexistence and, also, in the extent to which clutch laying can influence coexistence times in unstable systems. We wish to draw a careful distinction between prolonged but finite coexistence and formal stability. In what follows, we use *stable* to mean formal stability (infinite coexistence with mutual invasibility), while using *stabilize* to mean “prolong coexistence,” without implying that coexistence lasts infinitely long.

We proceed in three major steps. We establish the effects on coexistence of

changes in the number of available resource patches. Then we demonstrate important effects of changes in clutch sizes on coexistence times and on stability of competitive interactions. Finally, we explore the implications for coexistence of simultaneous changes in patch numbers and clutch sizes, which one would anticipate from the travel-costs argument (Heard 1998). There are important and surprising conclusions to be drawn from this integration of female behavior with the population and community ecology of competition in spatially structured landscapes.

MODEL AND RESULTS

The Basic Model

We took a simulation approach to the clutch-laying problem because this let us construct biologically interesting models without regard for analytical tractability. We considered the transient (short-term) behavior of our models to be as important as the existence or nature of equilibria, and analytical treatment of transient behavior is possible only for the simplest of models. We used a computer program written in QuickBASIC (Microsoft 1988) to examine the effects of clutch size and patch number on competitive coexistence in a system of discrete, ephemeral resource patches. In this model, all patches are identical, generations are nonoverlapping, and patches are renewed for each generation of competitors.

In each generation, the model begins with two populations of adults living on an array of P patches. Each adult is designated male or female with equal probability. (We therefore include in our model effects of random sex-ratio variation on the persistence of small populations.) For each female, a patch is chosen at random and a clutch of c eggs is laid there. A second patch is then chosen, also at random, and a second clutch (again of size c) is laid. This continues until an individual exhausts its egg supply and is repeated for each individual in each population. The choice of a patch is independent of whether, or how many, other conspecific or heterospecific females have oviposited there. We assume here that each female begins with a fixed egg supply and cannot replace eggs that are laid. This assumption is violated by drosophilids but met by many other insects (Büning 1994). We have not yet modeled renewable egg supplies, but since we do not allow individuals to die before their fecundity is exhausted, we would not expect strong differences from a renewable-egg model.

Once all individuals of both species have laid their eggs, a modified Hassell-Comins competition equation (Hassell and Comins 1976) is used to determine the numbers of emergent adults. Let $y_{1,i}$ and $y_{2,i}$ be the yield of emergent adults from patch i for species 1 and 2, respectively; these adults are the survivors of the $e_{1,i}$ eggs of species 1 and the $e_{2,i}$ eggs of species 2 that were laid (by all females) in that patch. Then

$$y_{1,i} = e_{1,i}(1 + a_1(e_{1,i} + \alpha_{12}e_{2,i}))^{-b_1}, \quad (1a)$$

where a_1 is a function of λ_1 , b_1 , and K_1 chosen such that the carrying capacity of each patch is K_1 :

TABLE 1
PARAMETERS FOR THE COMPETITION MODEL

Parameter	Meaning	Usual Value
P	Number of patches in system	100
K_s	Carrying capacity for species s , per patch	4
$N_s(0)$	Starting population size, species s	100
b_s	Shape of competition (scramble/contest), species s	1 (contest)
λ_s	Fecundity, species s	16
c_s	Clutch size, species s	4
a_s	Compound parameter: function of λ_1 , b_1 , and K_1	.21875
α_{12}	Interspecific competition strength: effect of species 2 on species 1	1
α_{21}	Interspecific competition strength: effect of species 1 on species 2	.5

$$a_1 = 2[(\lambda_1/2)^{1/b_1} - 1]/(\lambda_1 K_1). \quad (1b)$$

Parameters used in the model are defined in table 1, which also lists a standard set of parameter values used as a starting point for most comparisons. We show all equations for species 1; corresponding equations for species 2 are identical except with subscripts 1 and 2 reversed.

We chose to use a Hassell-Comins model because it is familiar and flexible and often fits field data well (Atkinson and Shorrocks 1981). Through modification of the shape parameters, b_1 and b_2 , it allows for a wide variety of competition functions ranging in shape from pure scramble through pure contest. The patterns we report, however, do not depend on the choice of a Hassell-Comins model but are robust to the use of other competition functions (S. B. Heard and L. C. Remer, unpublished manuscript; and see Ives and May 1985).

The Hassell-Comins equation can predict noninteger numbers of emergents, resulting in the existence of "fractional" individuals. We explored four alternative ways of treating these fractional individuals. First, we simply rounded the production of each patch to the nearest whole individual. Second, we let a fractional individual of size ϕ correspond to the production, with probability ϕ , of a whole individual. Third, we considered an "integrated-patch" model, in which the production from all patches was summed, and therefore fractional individuals emerging from different patches were combined into whole individuals (Atkinson and Shorrocks's 1981 model used this approach). Fourth, in our "pure-patch" model, we treated fractional individuals produced from each patch as independent individuals but with fecundity reduced in proportion to their fractional body size (only integer fecundities were allowed). This is not unrealistic, as insects subject to resource limitation commonly show reduced body size and consequently reduced fecundity (Atkinson and Shorrocks 1981; Heard 1994 and references therein). For patches of at least moderate size ($K > 2.5$), coexistence times differ little among these alternative models. We report results only for the pure-patch model, but none of the patterns we describe depend on the treatment of fractional individuals. (Even when patches are very small and so coexistence times are sensitive to the treatment used, comparisons among clutch sizes and resource densities are unaffected.)

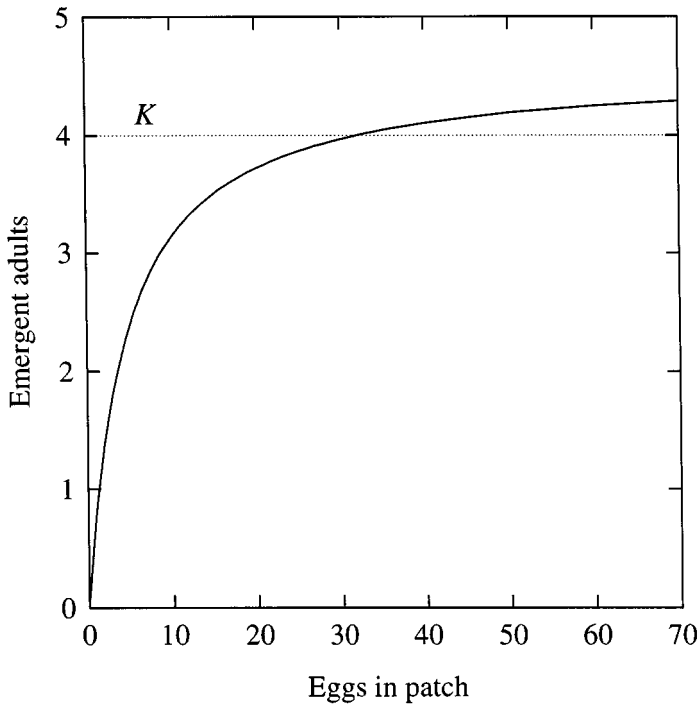


FIG. 1.—Emergence from a single patch as a function of colonization. Curve is for the Hassell-Comins model (eq. [1]), single-species case ($e_{2,i} = 0$), using $K = 4$, $b = 1$, $\lambda = 16$.

Note also that a female laying more than four eggs on a patch with a nominal carrying capacity of four emergent adults still receives a fitness return for doing so. This is because in the Hassell-Comins model the carrying capacity K is the number of emergents produced each generation by a one-patch system at equilibrium (found by rearranging eq. [1b]):

$$K_1 = 2[(\lambda_1/2)^{1/b_1} - 1]/(\lambda_1 a_1). \quad (2)$$

However, for any single patch in a multiple-patch system, the number of emergents increases with the number of colonists in a smooth, decelerating curve (fig. 1) extending beyond K . (The factors of two in eq. [2], which do not appear in the corresponding expression of Atkinson and Shorrocks 1981, arise from the fact that we explicitly considered the sex of each individual, allowing only females to lay eggs.)

After calculating emergent adults from all patches, our program recorded the number of individuals of each species and repeated the entire process for the next generation. The number of patches was held constant between generations, which means we assume that pressure from consumers does not regulate the dynamics of the patches themselves ("donor control"). This assumption is appro-

prate for many patchy resources (such as dung, carrion, mushrooms, fallen fruit) but not for others (live plants, hosts of parasites); we are currently investigating models in which patch density responds to consumer pressure.

A simulation ended either when one species became extinct or after 10,000 generations without extinction. We considered a species extinct when it was represented by fewer than two individuals (regardless of their body sizes). Our results do not depend on the precise definition of extinction. We report coexistence times in numbers of generations (before extinction of one species) averaged over 100 independent simulations.

At each generation, our program also calculated the population-level impacts of inter- and intraspecific competition on each species. We defined the impact of interspecific competition on one species as the proportional reduction in its population size inflicted by the presence of the other:

$$I_{1,\text{inter}} = 1 - \frac{\sum_i y_{1,i}}{\sum_i y_{1,i}|^{e_{2,i}=0}}, \quad (3a)$$

where $y_{1,i}|^{e_{2,i}=0}$ denotes the predicted yield of species 1 adults (from eq. [1]), had species 2 been absent. We then defined the total impact of competition on a species as the proportional reduction in its population inflicted by resource limitation and subtracted the interspecific impact to find intraspecific impact:

$$I_{1,\text{total}} = 1 - \frac{\sum_i y_{1,i}}{\sum_i e_{1,i}}, \quad (3b)$$

and

$$I_{1,\text{intra}} = I_{1,\text{total}} - I_{1,\text{inter}}. \quad (3c)$$

Note that while α_{12} , α_{21} , K_1 , K_2 , b_1 , and b_2 together specify the strength and form of interspecific and intraspecific competition within a patch, I_{inter} and I_{intra} measure the impacts of interspecific and intraspecific competition, respectively, at the population level. Impacts of competition are functions not just of the nature of within-patch competition but also of the distribution of larvae, of both species, over patches. Changes in larval distributions underlie the changes in competitive impacts and in coexistence discussed below.

Patch-Number Effects

We examined effects on coexistence of changing resource availability by varying the number of patches in the system. Each patch was of size 4 (parameters as in table 1, except P varying and starting population sizes of the two species K_1P and K_2P). All else being equal, coexistence times increase with the number of patches in the system, although at a decelerating rate in larger sys-

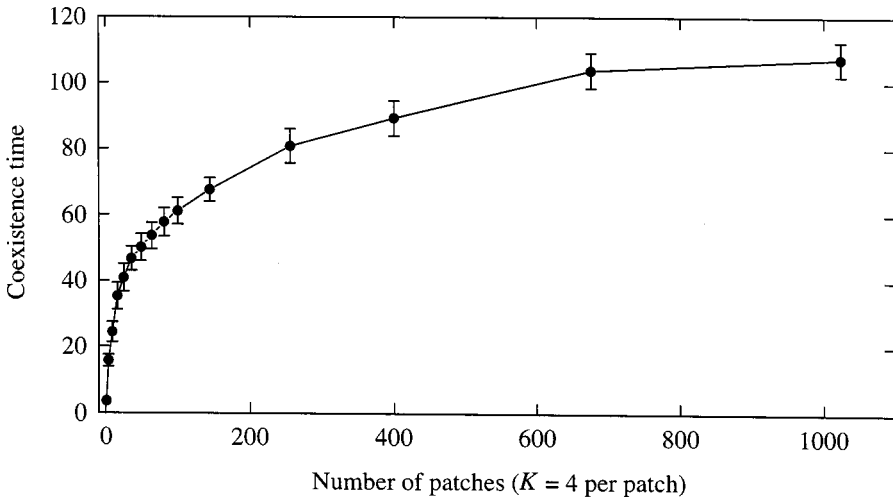


FIG. 2.—Coexistence times with increasing system size. Parameter values are as listed in table 1, except P varies. Symbols show means ± 2 SE (100 simulations per data point).

tems (fig. 2). This result is unsurprising and serves mainly as a reference point for results of models changing patch number and clutch sizes together (“Clutch sizes that respond to changes in patch numbers,” below).

Clutch-Size Effects

We examined clutch-size effects for equal and unequal competitors. For the equal competitors, we set $\alpha_{12} = \alpha_{21} = 1$ (other parameters as in table 1). For the unequal competitors we set $\alpha_{12} = 1$ and $\alpha_{21} = 0.5$ (other parameters again as in table 1), giving species 2 a moderate competitive advantage. Cases with stronger ($\alpha_{12} = 2$, $\alpha_{21} = 0$) and weaker ($\alpha_{12} = 1$, $\alpha_{21} = 0.7$) competition than considered here show the same qualitative clutch-size effects (S. B. Heard and L. C. Remer, unpublished data). In most cases, we allowed only those clutch sizes that evenly divided the total fecundity of a full-sized individual (16): $c = 1, 2, 4, 8$, or 16 eggs/clutch. We considered all possible combinations of those clutch sizes for the two competitors. However, for equal competitors with equal clutch sizes we also examined intermediate clutch sizes that force individuals to lay undersized final clutches of a few leftover eggs.

Changes in clutch size by one or both competitors have profound effects on coexistence, whether the competitors are equal or unequal. Only the strength (not the direction) of the effects vary with model parameters such as competition strength, patch size, system size, and so on.

Equal competitors.—For equal competitors ($\alpha_{12} = \alpha_{21}$), when clutch sizes are also equal (table 2, descending diagonal) the relative frequency of the two species fluctuates randomly (runs tests, not shown) until one species or the other

TABLE 2
COEXISTENCE TIME AND CLUTCH SIZE FOR EQUAL COMPETITORS

CLUTCH SIZE, SPECIES 1	CLUTCH SIZE, SPECIES 2				
	1	2	4	8	16
1	134 (14)	<u>82.3</u> (4.6)	<u>49.5</u> (2.2)	<u>27.3</u> (1.3)	<u>16.9</u> (.8)
2	80.6 (5.5)	145 (13)	<u>60.2</u> (2.6)	<u>31.5</u> (1.4)	<u>17.4</u> (.7)
4	48.4 (2.5)	59.6 (3.0)	182 (16)	<u>41.0</u> (1.9)	<u>19.4</u> (.9)
8	28.5 (1.5)	31.5 (1.5)	43.3 (2.4)	520 (53)	<u>26.6</u> (1.2)
16	16.6 (.6)	17.4 (.7)	20.3 (1.0)	26.0 (1.4)	2,442 (213)

NOTE.—All parameters as in table 1, except $\alpha_{12} = \alpha_{21} = 1$. Coexistence times are as follows: bold, either species excluded at random; underlined, species 1 excludes species 2; regular font, species 2 excludes species 1. Numbers in parentheses are twice the standard errors.

becomes extinct. For clutch sizes that divide the total fecundity into equal-sized clutches (1, 2, 4, 8, and 16), coexistence times increase smoothly as clutch size increases (fig. 3, *triangles*). Other clutch sizes, which have females laying a few leftover eggs in a final undersized clutch, show more complicated behavior (fig. 3, *circles*), with generally shorter coexistence times for clutch sizes midway between two even-divisor clutch sizes. To clarify other effects, we focus here on the even-divisor clutch sizes.

A difference in clutch size between equal competitors breaks their competitive deadlock and allows the competitor with the smaller clutch size to exclude the other (table 2, above and below diagonal) because it loses less of its fecundity to sib competition among clutch mates. The effects are strong, even for changes involving clutch sizes less than K .

Unequal competitors.—When one competitor is nominally superior, competitive exclusion can be dramatically delayed, prevented, or even reversed by changes in clutch sizes (table 3). When the two competitors' clutch sizes are equal (table 3, descending diagonal), increased clutch sizes delay competitive exclusion but do not prevent it. When the competitors' clutch sizes change independently (table 3, above and below diagonal), several outcomes are possible. We wish to highlight four important patterns.

First, when the inferior competitor increases its clutch size (e.g., table 3, col. 1), its exclusion is hastened. In the short term, when search and travel costs are high such behavior may nevertheless be favored by natural selection acting on individuals.

Second, a moderate increase in clutch size by the superior competitor delays, but does not prevent, competitive exclusion (e.g., table 3, row 1, first three entries). These delays can be substantial, and the effect is even stronger when the two competitors are more nearly equal in competitive ability.

Third, when the (nominally) superior competitor lays much larger clutches than does the (nominally) inferior competitor, extremely lengthy coexistence is

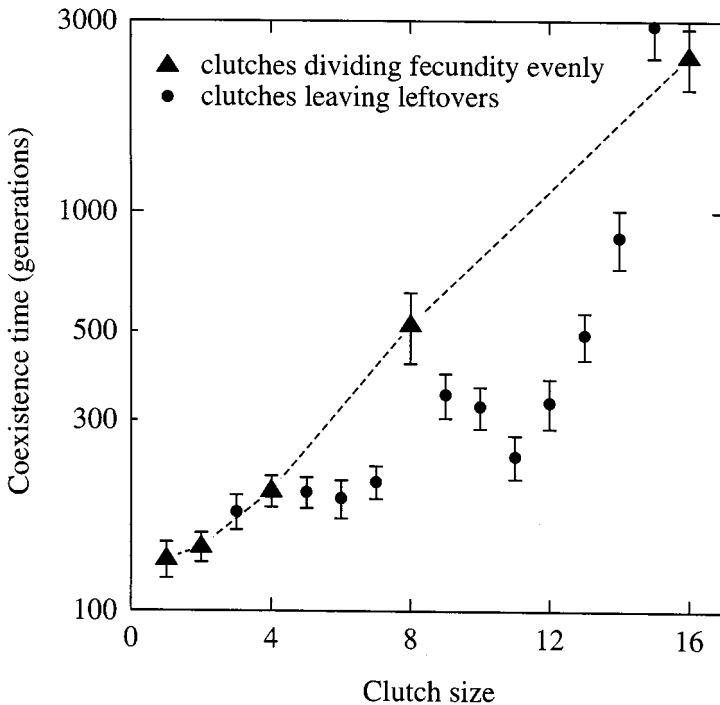


FIG. 3.—Coexistence times and clutch sizes, when the two species' clutch sizes are equal. Parameter values are as in table 1, except c_i varies and $\alpha_{12} = \alpha_{21} = 1$. Vertical axis is log-transformed. Symbols show means ± 2 SE (100 simulations).

possible ($>10,000$ generations; table 3, cases marked ∞). For these cases, coexistence is quasi-stable: coexistence is indefinite, and either species can invade a system populated only by the other, providing the initial population size of the invader is large enough to avoid stochastic extinction during the invasion (fig. 4). Formal stability is not possible in our models because they deal with finite populations, and therefore stochastic variation in demography must eventually lead to extinction (e.g., Nisbet and Gurney 1982). The competitor that normally persists at the lower population size (in most cases, the inferior competitor) has a somewhat more difficult time invading because its slower invasion means a higher risk of extinction while it is still rare (cf. two curves in fig. 4). In the appendix, we demonstrate analytically that clutch laying can lead to stable coexistence. This is important, because previous claims (Atkinson and Shorrocks 1981; Shorrocks and Rosewell 1988) of a similar effect have been shown to be false (Green 1986, 1988).

Finally, for large enough clutch-size differences, the outcome of competition can be reversed (table 3, rows 1–3, col. 5) the nominally superior competitor is excluded as a result of its clutch-size behavior (again, such large clutch sizes can still be favored by natural selection). This reversal has not been seen in pre-

TABLE 3
COEXISTENCE TIME AND CLUTCH SIZE FOR UNEQUAL COMPETITORS

CLUTCH SIZE, SPECIES 1	CLUTCH SIZE, SPECIES 2				
	1	2	4	8	16
1	40.1 (1.1)	50.1 (1.8)	92.3 (5.7)	∞	<u>341</u> (54)
2	41.2 (1.6)	51.1 (2.7)	86.0 (5.2)	∞	<u>1,042</u> (30)
4	35.6 (1.8)	39.6 (2.0)	61.2 (4.0)	9,882* (196)	<u>6,472*</u> (670)
8	24.3 (1.2)	26.2 (1.2)	33.3 (1.9)	97.2 (10.5)	∞
16	16.4 (.8)	16.2 (.7)	18.6 (.9)	25.5 (1.3)	189 (26)

NOTE.—All parameters as in table 1, except $\alpha_{12} = 1$, $\alpha_{21} = .5$ (species 2 superior). Coexistence times are as follows: underlined, species 1 excludes species 2; regular font, species 2 excludes species 1. Infinity symbols denote cases for which all 100 simulations ran 10,000 generations without exclusion. Numbers in parentheses are twice the standard errors.

* The coexistence time and the standard error are underestimates because some simulations had both species still extant after 10,000 generations.

vious treatments but is predicted by our analytical model (appendix). When travel costs are species-specific, and therefore optimal clutch sizes differ for the two competitors, such an outcome is not impossible.

For both equal and unequal competitors, clutch-size behavior influences the rate of competitive exclusion because it changes the balance between interspecific and intraspecific competition. All else being equal, an increase in clutch size by one competitor increases the impact of intraspecific competition on that competitor, while decreasing the impact of interspecific competition on the other. If this happens for the inferior competitor, competitive exclusion is hastened; but if it happens for the superior competitor, competitive exclusion is delayed. When both species increase clutch sizes, each sees an increase in intraspecific impact and a decrease in interspecific impact (fig. 5), and coexistence is on balance facilitated.

Clutch Sizes That Respond to Changes in Patch Numbers

The models outlined so far assume that clutch sizes and patch numbers change independently. However, if the (geographic) size of the landscape does not change, then patch numbers must be correlated with interpatch distances. Females are likely to pay increasing costs of search and travel as they move among more and more distant patches to lay their eggs. Therefore, clutch-size behavior should be under selection to respond to patch density. In particular, clutch sizes should increase when patches are scarce because a larger clutch size allows total fecundity to be distributed with fewer visits to patches. Such clutch-size adjustment appears to occur in natural populations of mushroom-breeding flies (*Drosophila recens* and *Drosophila subquinaria* [Drosophilidae] and *Megaselia rufipes* [Phoridae]; Heard 1998).

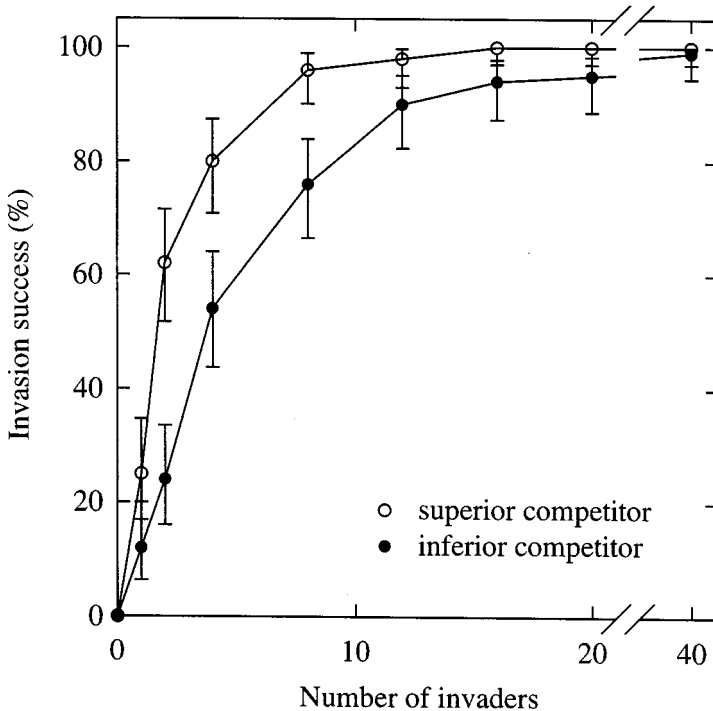


FIG. 4.—Success of invasions from rarity for a quasi-stable pair of competitors. Parameter values are as in table 1, except $c_1 = 4$, $c_2 = 8$. The independent variable is the starting population size for the rare competitor, invading a population of 400 ($= KP$) of the other species; “success” means increased population size of the invader after 30 generations. Symbols show success rates estimated from 100 replicate invasions, with 95% confidence intervals (from Rohlf and Sokal 1981).

We examined the consequences for coexistence of simultaneous changes in patch numbers and clutch sizes. For simplicity, we considered a single, persistent reduction in patch numbers. Results for a persistent increase in patch numbers would be opposite to those we show here. We began with a system of 160 patches and with clutch sizes of either one for each species or one for the inferior competitor and two for the superior (other parameters as in table 1). We ran a preliminary set of simulations to establish expected coexistence times (before competitive exclusion of species 1) for these parameter sets. We then imposed patch-number/clutch-size changes by letting a further set of simulations run roughly halfway to exclusion, at which point we cut the number of resource patches to a fraction $1/f$ of the original number ($f = 1, 2, 4, 8$, or 16). We let clutch sizes respond to the cut in patch numbers by a very simple rule:

$$c' = sfc, \quad (4)$$

where c' is the new clutch size, c the old clutch size, and s ($= 1/f, 1, 2$, or 4) is a parameter controlling the strength of the clutch-size response. For instance,

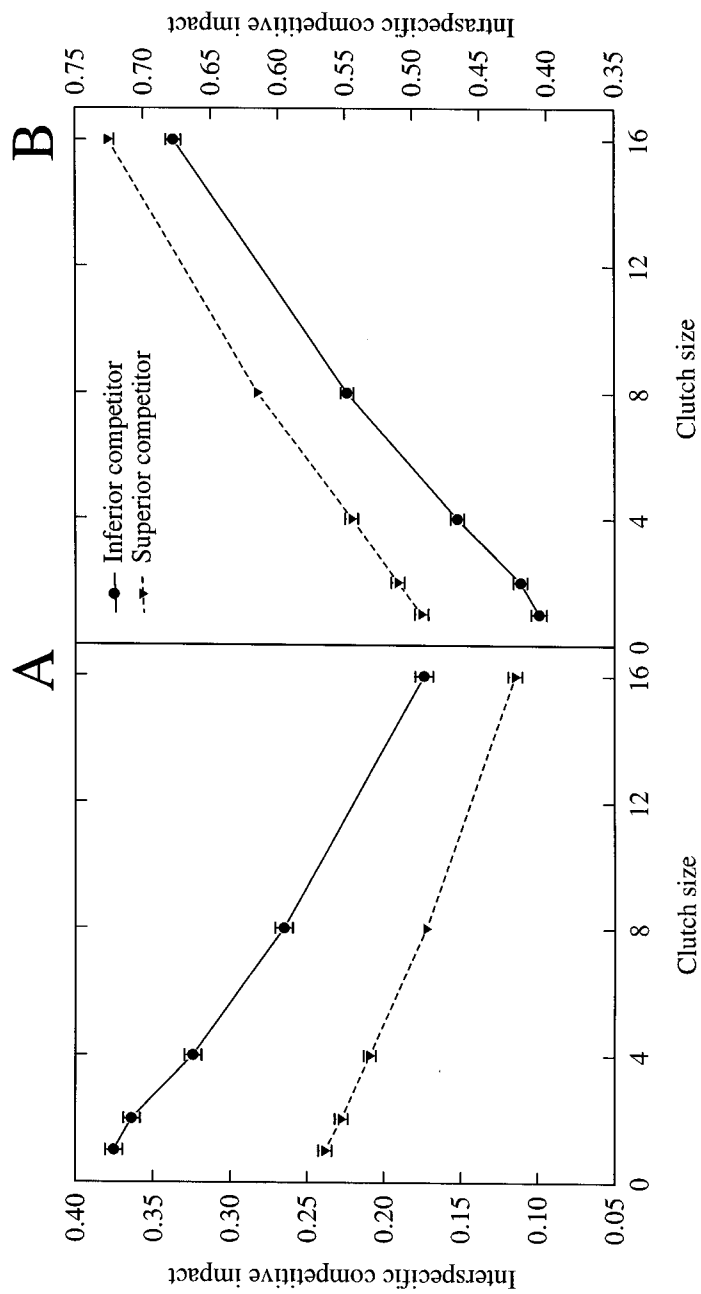


FIG. 5.—Changes in impact of competition with changing clutch sizes (see text for definition of *competitive impact*). Parameter values are as in table 1, except c_1 varies ($c_1 = c_2$); impacts shown are for generation 1 (offspring of starting adults). *A*, Interspecific competition. *B*, Intraspecific competition. Symbols show means ± 2 SE (100 simulations).

with $s = 1$, halving the number of patches doubles each species' clutch size. The number of clutches laid is decreased, but total fecundity is unaffected. We intended this to model the simplest possible response to resource availability. We do not doubt that clutch-size behavior in nature is more complex, but we are aware of no field data that would suggest any particular shape of response.

When clutch sizes increase in an adaptive response to declining patch numbers, there are two opposing effects on coexistence. In the short term, fewer patches means increased crowding of larvae in each patch (average $e_{1,i}$ and $e_{2,i}$ increase), and this tends to hasten competitive exclusion (fig. 2, and bottom curves in fig. 6). However, increasing clutch sizes change the distributions of $e_{1,i}$ and $e_{2,i}$, increasing intraspecific aggregation in such a way as to delay exclusion (table 3). The net effect of coexistence on a simultaneous change in patch numbers and clutch sizes depends on the starting difference between the two species' clutch sizes and on how strongly those clutch sizes respond to a reduction in patch numbers (fig. 6A, B). When the two species begin with equal clutch sizes, even a severe reduction in patch numbers can actually delay, rather than hasten, competitive exclusion, although a fairly strong clutch-size response is required to outweigh the effects of increased crowding (fig. 6A). When the superior competitor begins with a larger clutch size than the inferior, even a weak clutch-size response can make drastic cuts in patch numbers strongly stabilizing (fig. 6B).

These results are the direct opposite of the usual expectation (e.g., Wiens 1977; Schoener 1983; Grant 1986) that interspecific competition should be more severe, and competitive exclusion more likely, in regions or at times of resource scarcity. Prolonged coexistence with resource scarcity may be somewhat surprising, but it is explained by changes in the impacts of interspecific and intraspecific competition (fig. 7; cf. to impacts without any changes in clutch size or patch number, shown as dotted lines). For clarity, here we consider a case with a fairly strong clutch-size response: patch numbers cut from 160 to 40, and clutch sizes increasing from one to 16. In the very short term following the cut in patch numbers, and the increase in clutch sizes it provokes, the impacts of both interspecific and intraspecific competition increase for both competitors. Both increased crowding of the system and the increased clutch sizes contribute to the marked and rapid increase in intraspecific impact (fig. 7B). For interspecific impact, the effect of increased crowding is partly offset by the increased clutch sizes (which tend to decrease interspecific impact; fig. 5); however, a net increase is possible (fig. 7A).

These crowding effects are transitory, however, and so competitive exclusion need not be hastened. In the slightly longer term, population sizes drop rapidly to the new system-wide carrying capacity and then competitive exclusion proceeds at a new (sometimes slower) rate because of the new distribution pattern of larvae over patches (fig. 6). With all factors considered together, competitive impacts change over time in complex ways. Intraspecific impact remains higher for the inferior competitor (fig. 7B) not only because of its larger clutch size but also because exclusion has been slowed (fig. 6), and therefore its population density remains higher. For the superior competitor, however, intraspecific im-

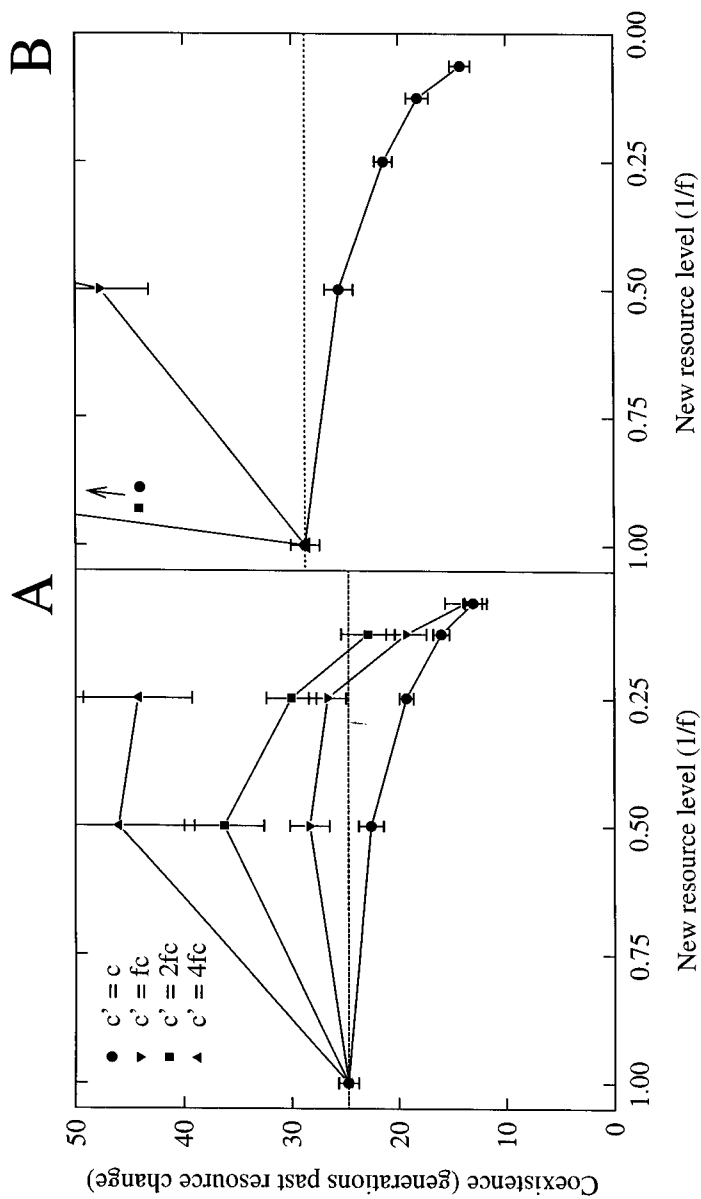


FIG. 6.—Effects on coexistence times of simultaneous changes in clutch size and patch numbers. Shown are four different clutch-size strategies in response to cuts in patch numbers. After 20 generations with a 160-patch system, patch numbers were cut to a fraction $1/f$ of their original numbers ($f = 2, 4, 8$, or 16); in response, each competitor adjusted its clutch-size behavior in accordance with one of four rules (c' , new clutch size; c , old clutch size). A, Initial clutch sizes 1 and 16. B, Initial clutch sizes 1 and 2 (superior). Symbols show means ± 2 SE (100 simulations).

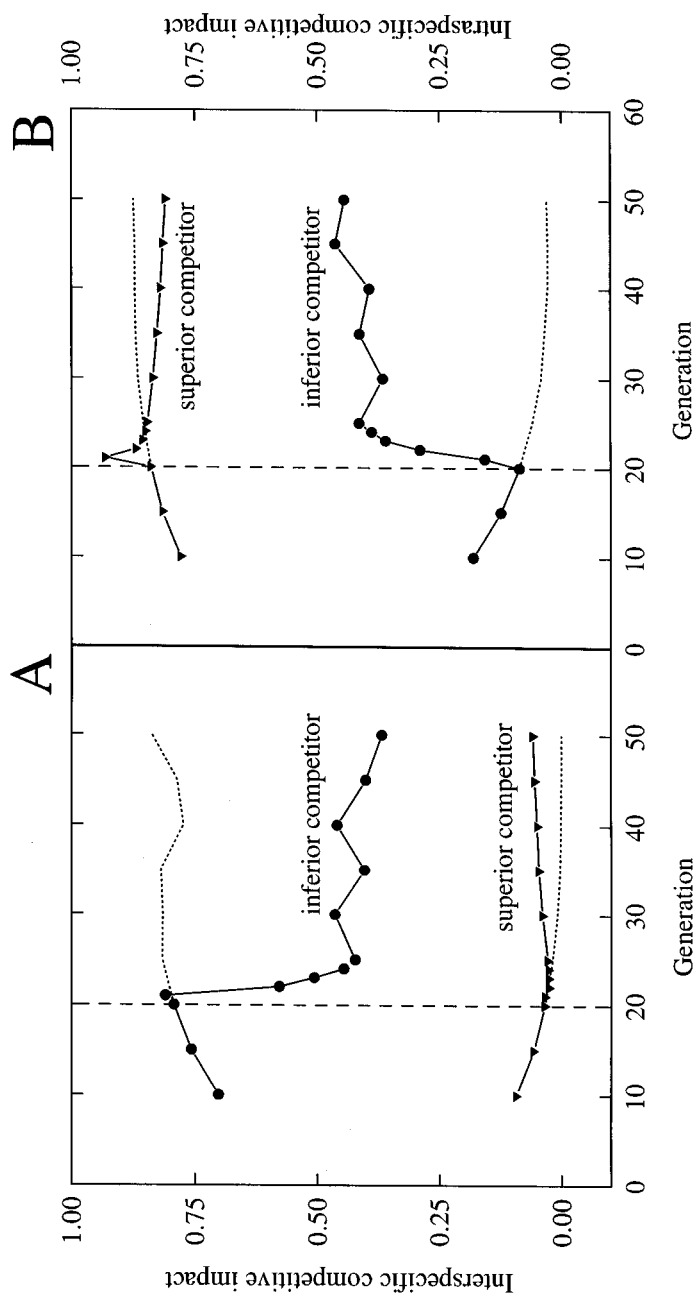


Fig. 7.—Changes in impact of competition with simultaneous changes in clutch size and patch numbers (see text for definition of competitive impact). Until generation 20, parameters as in table 1, except $P = 160$ and $c_1 = c_2 = 1$; after generation 20, $P = 40$ and $c_1 = c_2 = 16$. A, Interspecific competition. B, Intraspecific competition. Symbols show means ± 2 SE (100 simulations); error bars not shown are covered by symbols.

pact drops; although its clutch size has increased, its population density is reduced because it cannot so quickly exclude its rival. (Because it has a more aggregated distribution, its realized population size would also decline even if it were alone; see Ives and May 1985.) The same shifts in population densities reinforce the decline due to clutch size of interspecific impact on the inferior competitor and can actually overwhelm the effect of increased clutch sizes to strengthen the impact of interspecific competition on the superior competitor (fig. 7A). The net result of these changes in competitive impacts can be prolonged coexistence of the two competitors despite their decreased resource base. This pattern would be even stronger if we had included mortality of adults during their search for oviposition sites, as this further reduces population densities when patches are rare (Sevenster and van Alphen 1993).

DISCUSSION

Our results underline how the population dynamics and community ecology of consumers can be acutely sensitive to the spatial structure of the resource landscape and to the behavior of consumers as they exploit those resources. The predictions of spatially structured models can, in many cases, differ dramatically from predictions of nonspatial models (Levin 1974; Kareiva 1986; Hastings 1993; Tilman et al. 1994; Jansen 1995; Ferriere and Michod 1996). Our model makes predictions about competition and coexistence that are very different from what we might expect if we ignored spatial structure and oviposition behavior.

Can Clutch Laying Alone Lead to Stable Coexistence?

Clutch laying has been of great interest, among possible mechanisms for larval aggregation, because it should produce aggregation within, but not between, species. In turn, this should increase intraspecific competition and decrease interspecific competition, an effect that is generally stabilizing in competition models. However, the effect of clutch laying has been controversial, with conflicting claims about whether clutch laying can produce stable coexistence (Atkinson and Shorrocks 1981, 1984; Green 1986, 1988; Shorrocks and Rosewell 1988). No previous model has isolated the effect of clutch laying from other mechanisms for aggregation. Many such mechanisms have been suggested, including recruitment of females to pheromonally (Jaenike and James 1991) or physically (Atkinson 1983) marked patches, shared preferences for patch types (Beaver 1979a; Worthen and McGuire 1988; Ives 1991), and differences in detectability of patches (Ives 1991).

Atkinson and Shorrocks (1981) developed a simulation model of competition in which individuals were aggregated over patches in a negative binomial distribution, with constant clumping parameter k . They found that when k was small (strong aggregation) and patch size sufficiently small, prolonged or even stable coexistence was possible (formal stability confirmed analytically by Ives and May 1985). They suggested that the aggregation they modeled could be generated by clutch laying: if the number of adults visiting each patch is Poisson dis-

tributed and clutch sizes are logarithmically distributed, the distribution of eggs over patches is negative binomial. However, this form of clutch laying does not yield aggregation with a constant k (Atkinson and Shorrocks 1984; Green 1986); rather, aggregation is a decreasing function of the expected number of eggs per patch and therefore of population density. Real larval distributions do show such negatively density-dependent aggregation (Rosewell et al. 1990). In holding k constant, Atkinson and Shorrocks (1981) implicitly included a second, positively density-dependent, source of aggregation. This could only arise from clutch-size behavior if clutch sizes increase with population density. (The same is true of a more elaborate model [Atkinson and Shorrocks 1984] in which k is allowed to increase with population density but constrained to relatively small values.) We are aware of no theory or data suggesting such density-dependence for clutch sizes. In a related model, Ives and May (1985, app. E) considered the case in which clutch sizes were constant but the number of clutches per patch had a negative binomial distribution. This pattern of aggregation can also lead to stable coexistence, but once again clutch laying is not the only cause of aggregation: somehow, ovipositing females must be aggregated over patches to make the distribution of clutches negative binomial.

Our model differs from those of Atkinson and Shorrocks (1981, 1984) and Ives and May (1985) in that we treat clutch size explicitly and in that we allow no aggregation other than that due to clutch laying. Our model is therefore more restrictive and allows us to examine effects of clutch laying independent of any other kinds of aggregation. Green (1986, 1988) claimed that when aggregation is purely a result of clutch laying, stable coexistence is not possible (he did not address effects on coexistence times short of formal stability). However, Green made the critical assumption that the two competitors have identical clutch-size distributions (Green 1986, p. 302). Indeed, when clutch sizes are large but equal in our model, competitive exclusion is not prevented (table 3, descending diagonal, and see the appendix). The equal-clutch-size assumption is overly restrictive, though; we would often expect pairs of competitors to differ in clutch sizes, and when they do, Green's argument is invalid. In fact, when the superior competitor's advantage is balanced by a sufficiently larger clutch size, stable coexistence of competitors is possible. Our results show quasi-stability for such cases: indefinite coexistence in most or all runs (table 3), and invasibility of each species by the other given enough invaders to avoid stochastic extinction (fig. 4). In the appendix, we provide an analytical confirmation of this result. Clutch laying alone can produce stable coexistence in an otherwise unstable system but only when the better competitor also has the larger clutch size (see Hanski 1987 for one real case in which this is true).

The Importance of Short-Term Coexistence

While formal stability arising from clutch laying would be sufficient to explain the coexistence of competitors in natural systems, it is probably not necessary. Changes in clutch sizes that do not confer formal stability can nevertheless be strongly stabilizing; that is, they can greatly delay competitive exclusion. In

turn, this delay may provide time for other stabilizing mechanisms to come into play (Huston 1979)—for instance, reversals in relative competitive ability with environmental perturbations, or interruptions in competitive exclusion by occasional disturbance. When models suggest transient dynamics that last longer than the expected timescales of environmental perturbations (or even the timescales on which species associations change or life histories evolve; see, e.g., Jablonski and Sepkoski 1996), equilibria may never be attained in the real world. If so, the existence and stability properties of those equilibria are of little interest (Hastings and Higgins 1994; Heard 1995). Stability should not be seen as an all-or-none phenomenon; we must also consider quantitative changes in the rate of competitive exclusion (Huston 1979).

We have shown dramatic changes (sometimes 10-fold or more) in coexistence times with changes in clutch-size behavior, even when these changes do not produce stability. We can therefore confirm the suggestion of Atkinson and Shorrocks (1981, 1984) that aggregation resulting from clutch laying is stabilizing and can be, in theory, a powerful factor contributing to the coexistence of competitors in patchy ephemeral systems.

Clutch Laying and Coexistence in Nature

While aggregation resulting from clutch laying can stabilize competition in theory, its importance in stabilizing competition in nature remains to be established. This will depend in part on whether natural populations are spatially structured in ways consistent with our model and also on whether competition is an important force in natural communities.

Insects exploiting patchy larval habitats often show strongly aggregated distributions (Atkinson and Shorrocks 1984; Kneidel 1985; Wellings 1987; Ståhls et al. 1989; Rosewell et al. 1990; Jaenike and James 1991; Kouki and Hanski 1995; Sevenster and van Alphen 1996). Although some of this aggregation is unrelated to clutch laying (Del Solar and Palomino 1966; Atkinson 1983; Worthen and McGuire 1988; Ives 1991; Morris et al. 1992), some clearly arises because females lay eggs in large clutches (Itô et al. 1982; Atkinson and Shorrocks 1984; Hanski 1987; Damman and Cappucino 1991; Morris et al. 1992; Agarwala and Dixon 1993). Hanski (1987) has even discussed the case of two carrion flies with the direct relationship between competitive ability and clutch size that our model requires for stability, although he did not test whether clutch-size differences were responsible for the coexistence he observed.

Our model assumes more, however, than that females lay eggs in clutches. We also assumed that females of each species visit patches independently of females of the other. This is true of some natural systems (Kuusela and Hanski 1982; Ives 1991; Heard 1998), although not of others (Worthen and McGuire 1988; Ståhls et al. 1989; Jaenike and James 1991; Sevenster and van Alphen 1996), where females of different species appear to share preferences for certain patches. (We caution, however, that the strength and even the existence of interspecific association will depend on the way the set of patches under consideration is defined; see e.g., Ståhls et al. 1989.) Interspecific aggregation, when it

occurs, is often much weaker than intraspecific aggregation (Ståhls et al. 1989; Shorrocks and Sevenster 1995), but this is not always true (Jaenike and James 1991).

A theoretical model including interspecific aggregation of ovipositing females has been examined by Ives (1988*b*; see also Shorrocks et al. 1990). Ives (1988*b*) considered the case in which single eggs or clutches of eggs of each species had a negative binomial distribution over patches, but there was positive covariance between the distributions for the two species. The stabilizing effect of intraspecific aggregation declined as covariance between species increased, but even strong positive covariance did not obviate the stabilizing effect. While Ives's (1988*b*) model does not directly address aggregation arising from clutch laying, we would expect similar effects of interspecific aggregation in our model.

The prevalence and intensity of competition in natural communities has been the subject of considerable debate (e.g., Diamond 1975; Connor and Simberloff 1979; Connell 1983; Schoener 1983; Strong et al. 1984; Denno et al. 1995). However, there is little doubt that insects using patchy, ephemeral resources are often subject to intense interspecific and intraspecific competition at the scale of an individual patch (Atkinson 1979; Peck and Forsyth 1982; Grimaldi and Jaenike 1984; Kneidel 1985; Hanski 1987, 1990; Ives 1988*a*; Morris et al. 1992; Blossey 1995; Kouki and Hanski 1995; Prinkkilä and Hanski 1995). Furthermore, when patchiness is experimentally eliminated (by combining artificial baits or by using artificially large resource units), interspecific competition can be dramatically strengthened (Kneidel 1985; Shorrocks 1991*a*, 1991*b*; Kouki and Hanski 1995)—indicating that it would be intense but for factors, like clutch laying, that reduce interspecific association.

Because both clutch laying and competition are widespread among insects exploiting patchy ephemeral resources, it would seem that clutch laying has the potential to be an important stabilizing factor. However, establishing the role of clutch laying in delaying or preventing competitive exclusion in nature would mean comparing results of competition when clutch sizes vary independently from other forms of aggregation. We know of no such data, and therefore, we cannot yet say whether aggregation as a result of clutch laying significantly stabilizes communities of real competitors.

Implications of Adaptive Clutch-Size Behavior for Community Dynamics

If clutch size is subject to behavioral modification, we should expect changes in clutch size in response to changes in the resource environment. Almost any resource in the real world will show temporal changes in abundance, and many show dramatic changes (e.g., Harper 1981). Therefore, adaptive clutch-size behavior may have important implications for the community structure of consumers exploiting patchy, ephemeral resources.

Previous discussions of competition for temporally variable resources have held that interspecific competition should be most intense, and therefore competitive exclusion quickest, when the resource is rare (Wiens 1977; Dunham 1980;

Rotenberry and Wiens 1981; Smith 1981; Schoener 1982, 1983; Grant 1986). While this expectation is intuitively appealing, explicit consideration of spatial structure and adaptive behavior can lead us to expect, in some cases, exactly the opposite. Our results show that decreases in resource availability, when clutch sizes change in response, can actually ease competition and prolong coexistence (fig. 6). The direction and strength of the effects of changes in resource abundance depend on the magnitude of the resource changes and on the strength of the clutch-size response to those changes. This means that predictions for differences in guild size through time as resource abundance fluctuates (or among different resource types differing in abundance) are not as simple as they might appear when spatial structure and individual behavior are neglected. In many cases, diversity may be most easily maintained when resources are scarce—a result for competition reminiscent of Rosenzweig's (1971) paradox of enrichment for predator-prey systems.

Are these clutch size–patch density responses important in the real world? We cannot yet answer this question, but at least some of the basic assumptions of our model are met in real systems. Mushroom-breeding flies of several species show changes in aggregation patterns with changes in patch density that are consistent with the kind of clutch-size response we consider here (Heard 1998). Associations between travel costs (or variables correlated with travel costs) and either clutch size or patch selectivity have been reported from a variety of insects (Jackson 1966; Benson et al. 1975; Roitberg et al. 1982; Roitberg and Prokopy 1983; Waage and Ng 1984; Courtney 1986; Messina 1991). However, no data exist to indicate the strength of clutch-size responses to patch density when such responses occur, so we do not know how often competitive exclusion should be delayed, and how often it should be hastened, by resource scarcity.

The predictions of our model have important implications for conservation biology because they lead us to expect differences in the responses of consumer community dynamics to resources that are “rare” in different ways (Rabinowitz 1981). Patches may become rare because their density is reduced, although they are still distributed over a landscape of the same size; or alternatively, they may still occur at the same density but occur over a smaller landscape. In the former case, we would expect the kind of clutch-size response that could counteract the decline in the resource base and maintain or even prolong the coexistence of competing consumers, but in the latter, we would expect only accelerated exclusion and loss of consumer diversity. Decreased patch abundance resulting from loss or fragmentation of the habitat in which patches occur, then, could have much more serious consequences for consumer diversity than a similar decrease resulting from an overall decline in habitat quality. In turn, different conservation strategies would be appropriate for consumer communities in these two circumstances.

Although our model focuses on competitive interactions among consumers, adaptive clutch-size behavior may have consequences for other kinds of interspecific interactions as well. As the consumers we consider here become more aggregated in response to the declining density of their resource patches, preda-

tors and parasitoids could show either increased or decreased efficiency in attacking those consumers (recruiting either in density-dependent or inverse density-dependent fashion [Stiling 1987] to local aggregations of consumers). Predator pressure could therefore increase or decrease as consumer densities fall, and these possibilities have obvious implications for the stability of tritrophic interactions and for the design and implementation of strategies for the biological control of pest insects.

Finally, we have modeled a donor-controlled system, where the appearance of patches is independent of their exploitation. However, in many patchy systems (e.g., host plant–herbivorous insect communities), resources are self-renewing and resource patch density will respond to the intensity of consumer attack. When this is true, we suspect that adaptive clutch-size behavior may stabilize consumer-resource dynamics. Such stabilization would be possible if, for instance, a rare host plant population suffers reduced herbivory at the population level because its consumers lay fewer, larger clutches and therefore concentrate their attack on a few individuals. We are currently examining this possibility further with models that relax the donor-control assumption.

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APPENDIX

CONDITIONS FOR STABLE COEXISTENCE VIA CLUTCH LAYING

Some controversy has existed over whether clutch laying, alone, can allow the stable coexistence of two competitors that could not coexist if they laid eggs singly. Green (1986) established that clutch laying never allows stable coexistence if the two competing species show identical clutch-size behavior. Here we extend Green's argument to the case of two species with different clutch sizes and show that stable coexistence is possible in at least some models. This analytical treatment parallels our finding, in simulations, of mutual invasibility and indefinite persistence for some combinations of clutch sizes and competitive abilities. However, while our analytical model is closely related to our simulation model, they are not equivalent. Our general approach here is to demonstrate that coexistence due to aggregation from clutch laying is possible, not to derive a comprehensive set of coexistence criteria or to show a complete set of models for which coexistence occurs.

Consider two species competing over an array of ephemeral patches. Species *S* is the superior competitor, and species *I* is the inferior competitor. Coexistence requires that either species, when rare, can invade a population of the other species (at its single-species carrying capacity). Assume that females of each species lay clutches of eggs at random over the array of patches, with clutch sizes C_S and C_I (constants). The number of clutches per

patch is therefore Poisson distributed for each species. Competition occurs among larvae (clutch mates, other conspecifics, and heterospecifics) on each patch.

Our treatment here focuses on the total exposure to competition of a randomly chosen larva. By "exposure to competition" we mean the total number of individuals, of either species, with which an individual must compete. To take into account different intensities of intraspecific and interspecific competition, we express exposure as an equivalent number of conspecific competitors. (The impact of a specified level of competitive exposure on a larva depends on the shapes of the competition functions, and we address this dependency explicitly later in this appendix.) We follow closely the logic of Green (1986) in order to make clear how our treatment relates to earlier discussions of the issue (Atkinson and Shorrocks 1981; Shorrocks et al. 1990; Green 1986, 1988; Shorrocks and Rosewell 1988).

Let the effect of an S on an I be α_{IS} . This parameter is expressed relative to the effect of an I on an I , which we set as 1, and we assume that $\alpha_{IS} > 1$ (i.e., an individual I is hit harder by an S than by another I ; this reflects the competitive superiority of species S). Similarly, let the effect of an I on an S be α_{SI} , and assume $\alpha_{SI} < 1$ (an individual S is hit harder by another S than by an I). We assume that the carrying capacity of a patch is the same for each species, so that both α_{SI} and α_{IS} can be set relative to an intraspecific coefficient of 1. (If the carrying capacities differ, an additional constant must be added to the equations below.)

Now consider the expected competitive advantage, A , that the inferior competitor, when rare, has over the superior. A positive expected advantage ($A > 0$) means that a randomly chosen I individual is exposed to less competition than a randomly chosen S individual. When $A < 0$, the randomly chosen I experiences more competition than a randomly chosen S (i.e., I is at a disadvantage). A is defined over the universe of patches, but note that each patch will have a (stochastically) different number of competitors. Therefore, a positive expected advantage over an array of patches need not necessarily mean that the inferior competitor will increase relative to its competitor, and vice versa ($[A > 0] \leftrightarrow [dI/dt > 0]$). This implication does hold if $C_S = C_I$ (Green 1988), but otherwise, whether or not ($A > 0$) \leftrightarrow ($dI/dt > 0$) depends on the shape of I 's competition function (dI/dt vs. I , at the individual-patch scale).

For the time being we assume that competition functions are such that $A > 0$ implies that $dI/dt > 0$. This is not necessary for coexistence but simplifies our demonstration that coexistence is possible. There exist many reasonable competition functions that meet this assumption; we will show examples, but it is convenient to defer this until after specifying the form of the competitive advantage A . If ($A > 0$) \leftrightarrow ($dI/dt > 0$), a sufficient condition for coexistence is that each species has an advantage when rare: that is, $A > 0$ when the superior competitor is common but the inferior is rare, and $A < 0$ when the inferior competitor is common but the superior is rare. We need an expression for A .

Consider a randomly chosen "focal" individual of one species or the other. It shares its patch with conspecific and heterospecific competitors, which can be usefully divided into three sets: (1) clutch-mates; (2) individuals of species I from other clutches (i.e., excluding clutch mates if the focal individual is an I); and (3) individuals of species S from other clutches (i.e., excluding clutch mates if the focal individual is an S).

How many individuals will each set contain, and what are their contributions to the total competitive exposure of the focal individual? The key is that the number of clutches per patch (of each species) is Poisson distributed. As a result, the number of other conspecific clutches with which a randomly chosen clutch shares its patch has the same distribution as the number of clutches per patch (Green 1986). This simplifies our task, because in set 2, the number of clutches of I (call the expected number N_I) faced by our focal individual has the same distribution whether the focal individual is an I or an S . Similarly, in set 3, the number of clutches of S (call the expected number N_S) faced by our focal individual has the same distribution whether the focal individual is an I or an S . (This is only true for Poisson-distributed numbers of clutches; for other cases, the distributions of N_I and N_S would have

to be conditioned on the identity of the focal individual because either N_I or N_S excludes the clutch to which the focal individual belongs.)

Our focal individual, then, shares its patch with (1) either $C_S - 1$ or $C_I - 1$ clutchmates; (2) $N_I C_I$ larvae of species I in other clutches; and (3) $N_S C_S$ larvae of species S in other clutches. If our random individual is an I , the total exposure to competition is therefore

$$E_I = (C_I - 1) + (N_I C_I) + (\alpha_{IS} N_S C_S); \quad (\text{A1a})$$

if it is an S , the total exposure is

$$E_S = (C_S - 1) + (\alpha_{SI} N_I C_I) + (N_S C_S). \quad (\text{A1b})$$

In each expression, the three terms in parentheses correspond to the three sets of competitors as outlined above. We can now define the inferior competitor's expected advantage,

$$\begin{aligned} A &= E_S - E_I \\ &= (C_S - 1) + \alpha_{SI} N_I C_I + N_S C_S - (C_I - 1) - N_I C_I - \alpha_{IS} N_S C_S \\ &= (C_S - C_I) + (\alpha_{SI} - 1) N_I C_I + (1 - \alpha_{IS}) N_S C_S. \end{aligned} \quad (\text{A2})$$

However, since we are concerned with invasibility, we focus on cases where either S or I is rare, and so either N_I or N_S is nearly 0; also, we assume the species being invaded is near its carrying capacity (single-species equilibrium). Let N_I^* and N_S^* represent the expected number of clutches of I or S in a patch given a population of I or S near carrying capacity. Now:

$$A \approx (C_S - C_I) + (1 - \alpha_{IS}) N_S^* C_S \quad (\text{when } I \text{ is rare}) \quad (\text{A3a})$$

or

$$A \approx (C_S - C_I) + (\alpha_{SI} - 1) N_I^* C_I \quad (\text{when } S \text{ is rare}). \quad (\text{A3b})$$

When $A > 0$, the inferior competitor has an advantage over the superior and its relative frequency can increase (recall we are assuming a competition function such that $[A > 0] \leftrightarrow [dI/dt > 0]$). For coexistence, we need $A > 0$ when I is rare, and $A < 0$ when S is rare. This gives coexistence criteria

$$(C_S - C_I) > (\alpha_{IS} - 1) N_S^* C_S \quad (\text{A4a})$$

and

$$(C_S - C_I) < (1 - \alpha_{SI}) N_I^* C_I. \quad (\text{A4b})$$

Can these criteria be met? Note that because $\alpha_{IS} > 1$, the right-hand side of (A4a) is always positive. Green's (1986) result boils down to observing that when the clutch sizes C_S and C_I are equal, the left side of (A4a) is 0; therefore, that criterion cannot be met and coexistence is impossible. However, Green (1986) did not consider cases where $C_S \neq C_I$. When the superior competitor has the larger clutch size ($C_S > C_I$), the left-hand side of (A4a) is also positive and for appropriate values of α_{IS} , α_{SI} , N_S^* , and N_I^* it is possible to fulfill the two coexistence criteria. Clutch laying *can* produce stable coexistence.

It remains only to show that there exist competition functions that meet our assumption that $(A > 0) \leftrightarrow (dI/dt > 0)$. (A reader willing to accept this point can safely skip to the last paragraph.) Define N_{crit} = the value of N_S giving $A = 0$; from (A3a) we have

$$N_{\text{crit}} = (C_S - C_I) / [(\alpha_{IS} - 1) C_S]. \quad (\text{A5})$$

We require that dI/dt , the system-wide growth rate of the inferior competitor, be positive whenever $N_S > N_{\text{crit}}$. This growth rate, integrated over the stochastic distribution of S , is

$$\frac{dI_{\text{system}}}{dt} = \sum_n [P(n_S) \frac{dI_{\text{patch}}}{dt}(n_S)], \quad (\text{A6})$$

where $P(n_s)$ is the probability of a patch having n_s clutches of S given that the expected number is N_s :

$$P(n_s) = \frac{e^{-N_s}(N_s)^{n_s}}{n_s!}, \quad (\text{A7})$$

and $dI_{\text{patch}}/dt(n_s)$ is the growth rate for a single clutch of I in such a patch. Note again that because we are assuming I is rare, we can ignore the possible presence of more clutches of I . Using the interspecific competition coefficient α_{IS} , the number of clutches of I equivalent to n_s clutches of S is

$$n_I = \alpha_{IS} n_s C_S / C_I. \quad (\text{A8})$$

Assume that I has a logistic growth function, such that in a single patch

$$\frac{dI_{\text{patch}}}{dt} = rn_I(1 - n_I/K), \quad (\text{A9})$$

where r is the intrinsic growth rate for an inferior competitor. Now we substitute equations (A5), (A7), (A8), and (A9) into (A6) and find, numerically, parameters such that $dI/dt = 0$. There are many such parameter sets; two examples are ($C_S = 4$, $C_I = 2$, $r = 2$, $K = 4$, $\alpha_{IS} = 1.333333$) and ($C_S = 6$, $C_I = 2$, $r = 2$, $K = 4$, $\alpha_{IS} = 2$). Therefore, reasonable competition functions do exist for which ($A > 0$) \leftrightarrow ($dI/dt > 0$), and our use of A is justified (we stress, again, that such functions are not necessary for coexistence—only for algebraic convenience).

In summary, when clutch sizes are unequal, aggregation due to clutch laying *can* allow stable coexistence of competitors (contra Green 1986, 1988) for at least some values of the competition coefficients, carrying capacities, and clutch sizes and for some competition functions (recall the assumption about the form of the competition functions needed so that $A > 0$ really does assure invasion). For other competition functions, the coexistence criteria will be more complicated than (A4), and numerical or simulation methods will in general be required to demonstrate stability. In particular, we have demonstrated mutual invasibility (and therefore stable coexistence) for some parameter sets in the detailed model outlined in the main body of this article.

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