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COMPETITIVE EXCLUSION THROUGH REPRODUCTIVE INTERFERENCE

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SUMMARY

A simple differential equation model was developed to describe the competitive interaction that may occur between species through reproductive interference. The model has the form comparable to Volterra's competition equations, and the graphical analysis of the outcome of the two-species interaction based on its zero-growth isoclines proved that: (1) The possible outcome in this model, as in usual models of resource competition, is either stable coexistence of both species or gradual exclusion of one species by the other, depending critically upon the values of the activity overlapping coefficient c_{ij}; (2) but, for the same c_{ij}-values, competitive exclusion is much more ready to occur here than in resource competition; (3) and moreover, the final result of the competition is always dependent on the initial-condition due to its non-linear isoclines, i.e., even under the parameter condition that generally allows both species to coexist, an extreme bias in intial density to one species can readily cause subsequent complete exclusion of its counterparts. Thus, it may follow that the reproductive interference is likely to be working in nature as an efficient mechanism to bring about habitat partitioning in either time or space between some closely related species in insect communities, even though they inhabit heterogeneous habitats where resource competition rarely occurs so that they could otherwise attain steady coexistence.

KEYWORDS: insect community, competition, differential equation, mating interference, habitat partitioning.

INTRODUCTION

Recent studies on natural communities of insects have presented ample evidence showing that interspecific competition is not a major force determining their fundamental structures (Strong et al., 1984). This is particularly true in herbivores. In nature one may actually find many plant species which individually support many herbivorous insects sharing similar ecological niches (e.g., Kennedy and Southwood, 1984). Possible mechanisms to bring about such non-competitive coexistence of many similar-niched species have also been studied and discussed at length (e.g., Hairston, Smith and Slobodkin, 1961; Atkinson and Schorrocks, 1981; Strong et al., l.c.; Kuno, 1988).

This general principle does not usually hold, however, when the species concerned are closely related, in which case the species sometimes segregate their habitats or host plants rigidly from each other. Table 1, which was composed after Fukuda et al.'s (1982) description, presents some examples of such segregation as observed among Papilionid butteflies in Japan. It reveals that any two species comprising a very close pair (both taxonomically and in appearance) have different main host plants or otherwise have separated local distributions, and hence are regarded as virtually not sharing their basic habitats.

Phenomenologically, the habitat segregation in these cases might look as supporting the conventional competitive exclusion principle that assumes the interference due to limited resources (Hardin, 1960). In many herbivore guilds, however, the real effects of individual species to be imposed upon the host plant may not be so diverse as to generate considerable differentiation in accordance with taxonomical differences of the species, even though there are some differences in the site or time of feeding. A different mechanism of species exclusion may therefore need to be considered here.

The purpose of this paper is to show on a theoretical basis that the interference that occurs in mating or reproductive processes could be a powerful and universal mechanism to cause such competitive exclusion between closely related species. The idea that reproductive interference could by itself bring about competitive exclusion was first invoked by Ribeiro and Spielman (1986). To account for the parapatry between sibling species, they used a discrete-time population model that incorporates both the reproductive interference between species and the dispersal between populations. Based on a simpler, Volterra-type interaction model that allows a

Table 1. Differentiation of the main host plants in each pair of closely related species of Papilionid butterflies inhabiting Japan (after Fukuda et al., 1982).

Pair of closely related species	Main Host plants
Luedorphia japonica	*Heterotropa* spp.
L. puziloi	*Asiasarum Sieboldi*
Parnassius glacialis	*Colidalis incisa*
P. hoenei	*Colidalis ambigua**
Graphium sarpedon	*Cinnamomum Camphora*
G. doson	*Michelia compressa*
Papilio machaon	Several species of Umbelliferae
P. xuthus	Several species of Rutaceae
Papilio protenor	*Fagara ailanthoides*
P. macilentus	*Orixa japonica*
Papilio bianor	*Orixa japonica*
P. maacki	*Phellodendron amurense*

* *C. ambigua* is commonly eaten also by *P. gracialis* in Hokkaido district where both butterfly species are distributed, but their local distributions there are known to be virtually separated.

general comparison of the disturbing effect between different types of interaction, the present paper will extend and generalize their conclusion by proving that this type of interference may have a much stronger effect for the exclusion of their competitors than the usual competition for common resources.

THE MODEL

Unlike Ribeiro and Spielman (1986), I used here a model of a differential rather than a difference equation type. This is simply to assure both generality and simplicity for the model. The base equation we employed is therefore the logistic model in the form, $\mathrm{d}N/\mathrm{d}t = bN - dN - hN^2$, where b and d are birth and death rates and h represents the crowding effect to be imposed per individual on others (see Kuno, 1991 for the reason of using this form). I assumed, like Ribeiro and Spielman (l.c.), that the interference between the coexisting species is to occur only through the reproductive or mating process and hence to affect the birth rate only of each species as a diluting effect. The resultant model for describing the two-species competition is

$$\begin{cases} \dfrac{\mathrm{d}N_1}{\mathrm{d}t} = \left\{ b_1\left(\dfrac{N_1}{N_1 + c_{12}N_2}\right) - d_1 \right\} N_1 - h_1 N_1^2 \\ \dfrac{\mathrm{d}N_2}{\mathrm{d}t} = \left\{ b_2\left(\dfrac{N_2}{N_2 + c_{21}N_1}\right) - d_2 \right\} N_2 - h_2 N_2^2 \end{cases} \tag{1}$$

where c_{12} (c_{21}) is the competition coefficient that indicates the relative intensity of interfering effect of species 2 (1) on 1 (2) due to overlapping in reproductive activities.

The model of usual competition for the common resource to be contrasted with this is the well-known Volterra equations,

$$\begin{cases} \dfrac{\mathrm{d}N_1}{\mathrm{d}t} = (b_1 - d_1)N_1 - h_1(N_1 + c_{12}N_2)N_1 \\ \dfrac{\mathrm{d}N_2}{\mathrm{d}t} = (b_2 - d_2)N_2 - h_2(N_2 + c_{21}N_1)N_2 \end{cases} \tag{2}$$

where c_{12} (c_{21}) is the competition coefficient as above but it expresses here the overlapping in resourse consuming activities.

The zero-growth isoclines for species 1 and 2 for Eq. (1) are respecitively

$$\begin{cases} N_2 = \dfrac{1}{c_{12}}\left(\dfrac{b_1 N_1}{d_1 + h_1 N_1} - N_1\right) \\ N_1 = \dfrac{1}{c_{21}}\left(\dfrac{b_2 N_2}{d_2 + h_2 N_2} - N_2\right) \end{cases} \tag{3}$$

which are comparable to those for Eq. (2) for usual resource competition,

$$\begin{cases} N_2=\dfrac{1}{c_{12}}\left(\dfrac{b_1-d_1}{h_1}-N_1\right) \\ N_1=\dfrac{1}{c_{21}}\left(\dfrac{b_2-d_2}{h_2}-N_2\right) \end{cases} \tag{4}$$

CONDITIONS FOR EXCLUSION OR COEXISTENCE OF SPECIES

Using the zero-growth isocline formulas derived above, we can now analyze graphically the outcome of the two-species interaction in this model. A characteristic feature of the isoclines as described by Eq. (3) is that they draw concave curves on both axes (see Fig. 1A–D), not straight lines as in Eq. (4) for the Volterra model (Fig. 1E–H).

This brings considerable complexity to the process of competitive interaction for both species, though the final result will be one of these three: (a) species 1 out-competes sp. 2; (b) species 2 out-competes sp. 1; or (c) both species attain stable coexistence. The important conclusions deduced from this analysis to characterize the reproductive competition in contrast to the usual resource competition are as follows.

(1) The outcome of the competition is always dependent on the initial density condition. Namely, even when either species has much higher ecological capacity in terms of either $r(=b-d)$ or $1/h$ than its counterparts, there always exists a certain area in the N_2-N_1 graph that leads the latter (weaker) species to win (Fig. 1D). Also, even under the condition that allows both species to coexist as in Fig. 1A, either species can be readily excluded if the initial density ratio is extremely biased. This means that the stability here can no longer be global. Such uncertainty of the competition outcome is evidently specific to the reproductive competition.

(2) The possibility of stable coexistence of both species increases steadily as the activity overlapping coefficient c_{ij} is decreased, but for the same c_{ij}-value it is considerably lower than the conventional resource competition model (compare Fig. 1A–D with E–H respectively). Namely, competitive exclusion is much more ready to occur in reproductive interference than in resource competition.

(3) The possibility of stable coexistence is dependent also on the reproductive rate of both species, becoming higher either as birth rate b increases or as death rate d decreases. This property also is peculiar in reproductive competition (see Fig. 2).

SOME EXTENSIONS TO THE MODEL

It is easy to extend the two-species model (1) to include three or more (k) species interactions by rewriting (1) as a set of k equations each desecribed as

$$\frac{dN_i}{d_t}=b_i\left(\frac{N_i}{N_i+\sum_{j\neq i}c_{ij}N_j}\right)N_i-d_iN_i-h_iN_i^2 \tag{5}$$

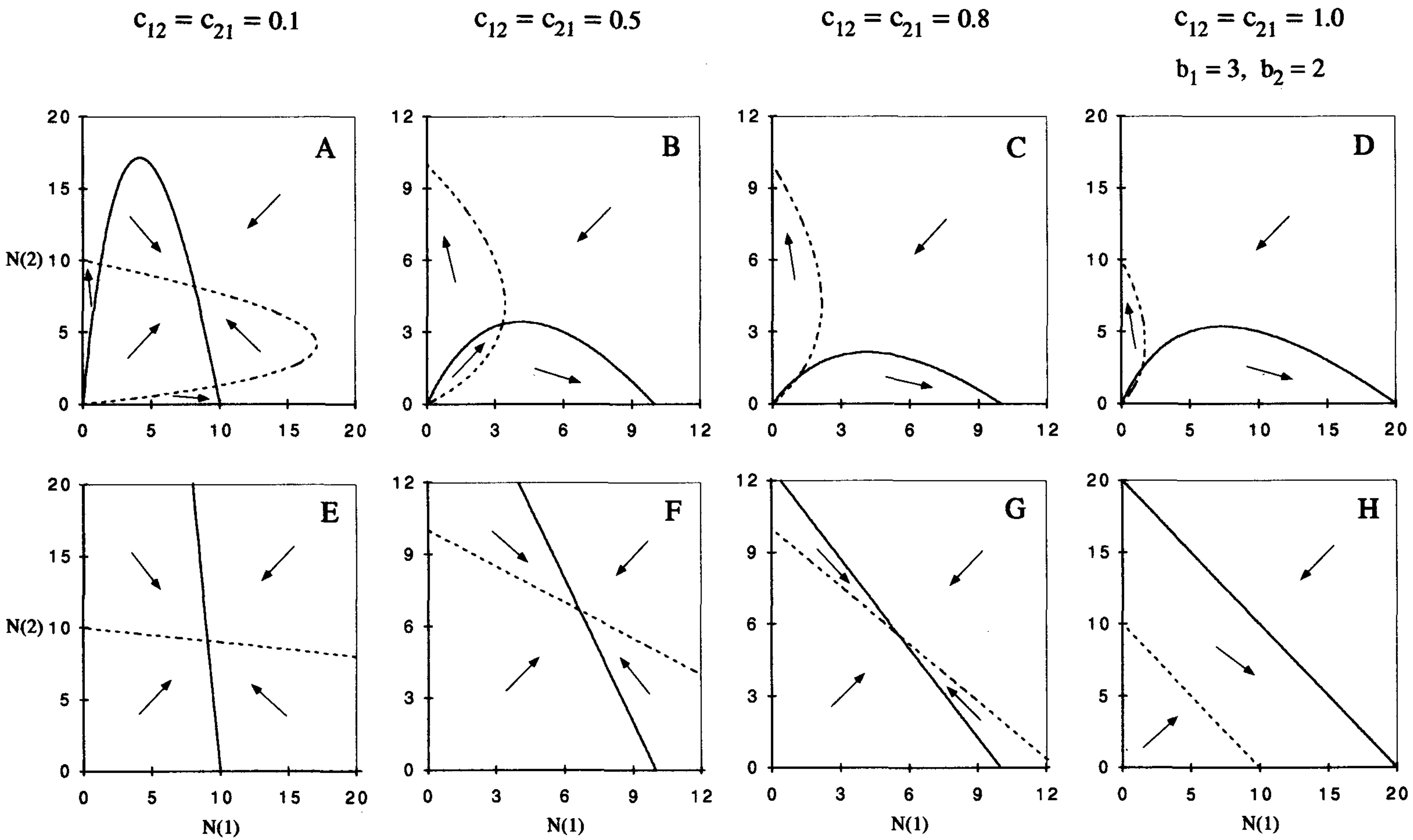

Fig. 1. Comparison of the zero-growth isoclines for assessing the competition outcome between the models for the reproductive interference (A to D from Eq. (3)) and for the usual resource competition (E to H from Eq. (4)) for respective values of the competition coefficient c_{ij} ($b_1 = b_2 = 2$, $d_1 = d_2 = 1$, $h_1 = h_2 = 0.1$). The solid and the broken lines represent the isoclines for N_1 and N_2, respectively.

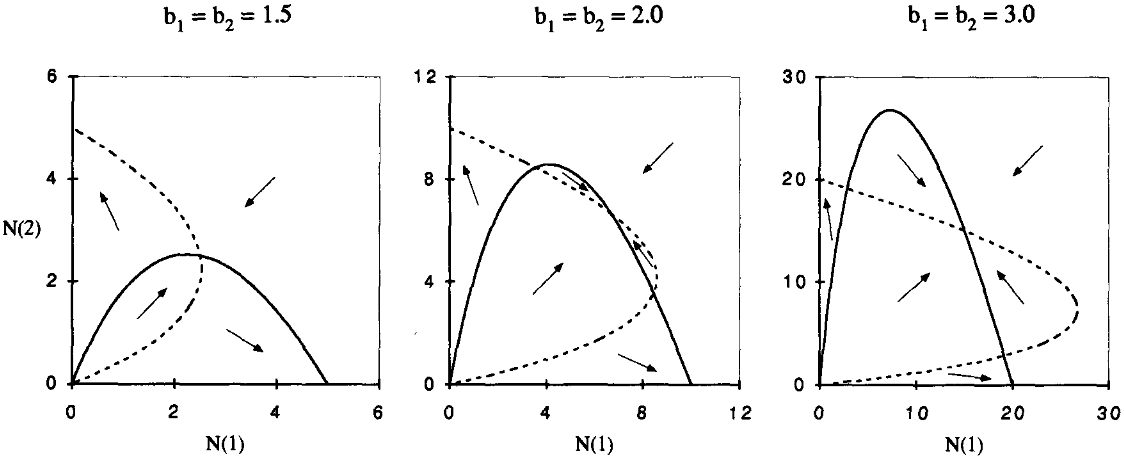

Fig. 2. Effect of the varying reproductive rate on the zero-growth isoclines for assessing the competition outcome in the reproductive interference model (Eq. (3); $d_1 = d_2 = 1$, $h_1 = h_2 = 0.1$, $c_{12} = c_{21} = 0.2$). The solid and the broken lines represent the isoclines for N_1 and N_2, respectively.

where c_{ij} now represents the competition coefficient of species j upon species i. For $k > 2$ the isocline analysis of the condition for coexistence becomes difficult, but by solving these simultaneous equations numerically we can readily see that the above features of the reproductive interactions apply to the general k-species cases as well. An example of the competition outcome for $k = 9$ is shown in Table 2 in comparison with the outcome of the resource competition as obtained from

$$\frac{dN_i}{d_t} = b_i N_i - d_i N_i - h_i \left(N_i + \sum_{j \neq i} c_{ij} N_j \right) N_i \tag{6}$$

under the same parameter conditions. For simplicity, the interspecific overlapping in reproductive niche was assumed here to be one-dimensional so that $c_{ij} = 0.2$ only between neighbouring species (i.e., for $j = i + 1$) and otherwise $c_{ij} = 0$. From the table we can see that the reproductive interference soon brought about complete parapatry or segregation of activity within the guild by eliminating the four speices which happened to have been intermediately situated, despite that the rate of niche overlapping here is so low that no exclusion occurs at all in the corresponding resource competition model.

It is also easy to combine the two models (5) and (6) to express the situation that interspecific interactions occur in both reproductive and resource-cosuming processes, i.e.,

$$\frac{dN_i}{d_t} = b_i \left(\frac{N_i}{N_i + \sum_{j \neq i} c_{ij} N_j} \right) N_i - d_i N_i - h_i \left(N_i + \sum_{j \neq i} c'_{ij} N_j \right) N_i \tag{7}$$

in which case joint effects of the interference make stable coexistence of the species

Table 2. Outcomes of the competition among the hypothetical 9 species in models (5) and (6) ($b_i=2$, $d_i=1$, $c_{i,j}=0.2$ for $j=i+1$ and $c_{i,j}=0$ for $j\neq i+1$).

(a) Reporoductive competition (Eq. (5)).

Time	Population density of each species								
t	N_1	N_2	N_3	N_4	N_5	N_6	N_7	N_8	N_9
0	10.0	10.0	10.0	10.0	10.0	10.0	10.0	10.0	10.0
1	8.2	6.7	6.8	6.8	6.8	6.8	6.8	6.7	8.2
5	8.3	2.9	5.2	4.4	4.7	4.4	5.2	2.9	8.3
10	9.8	0.1	8.2	2.0	6.3	2.0	8.2	0.1	9.8
20	10.0	0.0	10.0	0.0	10.0	0.0	10.0	0.0	10.0

(b) Resource competition (Eq. (6)).

Time	Population density of each species								
t	N_1	N_2	N_3	N_4	N_5	N_6	N_7	N_8	N_9
0	10.0	10.0	10.0	10.0	10.0	10.0	10.0	10.0	10.0
1	9.0	7.9	8.0	8.0	8.0	8.0	8.0	7.9	9.0
5	8.6	6.9	7.2	7.2	7.2	7.2	7.2	6.9	8.6
10	8.6	6.8	7.2	7.1	7.2	7.1	7.2	6.8	8.6
20	8.6	6.8	7.2	7.1	7.2	7.1	7.2	6.8	8.6

even more difficult.

Further extension to the combined interaction model (7) may be possible by assuming that the interspecific mating can produce offspring that are sterile but sexually active. Here, the model for two-species interaction should include three simultaneous equations, the third one describing the density of the hybrid population. Though this extension may make the model much more complex, it may not bring about any fundamental changes to the principles of reproductive competition that were derived from the original model.

Discussion and Conclusions

In view of the knowledge accumulated so far on natural insect communities, we may now be able to characterize the interspecific relationship among phytophagous insects with the following principles.

(1) Many species usually share a similar ecological niche on the same host plant, and yet they have attained stable coexistence.

(2) Taxonomically very close species often show definite segregation of host plants or habitats from each other.

(3) In the cases where very close species share the same habitat or host plant, definite mutual isolation in either space or time has usually been attained in their mating processes.

Many examples supporting principle (3) beside (1) and (2) may be found among

Table 3. Main host plants and male's flight activity period of the day in the 7 Lycaenid butterflies of genus *Favonius* inhabiting Japan (after Fukuda et al., 1983).

Species	Main host plants	Flight period of the day
Favonius yuasai	*Quercus acutissima*	At dawn and evening
F. orientalis	*Q. serrata*	Morning
F. saphirinus	*Q. dentata* and *Q. aliena*	Evening
F. ultramarinus	*Q. dentata*	Afternoon
F. latifasciatus	*Q. aliena*	Morning
F. jezoensis	*Q. crispula*	Afternoon to evening
F. cognatus	*Q. crispula*	Morning

natural communities of insects, though they seem to have rarely been discussed so far in the context of interspecific competition. Table 3 shows a clear example of such time-sharing system observed among Japanese Lycaenid butterflies of genus *Favonius* (after Fukuda et al., 1983). These insects feed on several *Quercus* trees and each host species supports two or more butterfly species. But we see here that among each set of species inhabiting the same host plant species (i.e., *F. jezoensis* and *cognatus* on *Quercus crispula*, *F. ultramarinus* and *saphirinus* on *Quercus dentata*, or *F. saphirinus* and *latifasciatus* on *Quercus aliena*), separation of the male's flight activity period of the day is always complete. These Lycaenids are thus regarded to have succeeded in avoiding reproductive interference by separating either their host plant or their flight period of the day from each other. The separation among related species can also be realized by differentiating the period of seasonal occurrence as seen in many sets of insect species living in the same place. The problem of reproductive interference might look even more serious among nocturnal insects that use specific chemicals (sex pheromones) for sexual communication, since the chemicals for use in communication may inevitably become similar among related species. But evidence has now been accumulated which shows that many of nocturnal moth species use two or more chemicals in mixture for communication and by differentiating their proportions they are effectively avoiding mutual interference to secure their stable coexistence (e.g., Tamaki, 1977).

The result of the present study seems to have provided a reasonable explanation to many of these empirical facts. The model demonstrated how seriously the interference in adult reproductive processes may disturb the population maintenance of both the species. The inherent uncertainty or the initial-condition dependence of the competition outcome revealed here may be of particular significance, since it means that in this type of competition, a higher ecological ability (i.e., higher r or lower h in the logistic) no longer guarantees one-sided dominance of the species to its rival. Theoretical investigations on the population interactions when only resource competition is at work have so far shown that the stable coexistence of similar-niched species is rather ready to occur when the habitat as a whole is (as is usual) spatially heterogenious (Kuno, 1988), or when natural enemies or other factors effectively control populations of individual species at low densities (Strong et al., 1984). We may thus conclude that whether a given insect species can coexist steadily with its allied counterparts depends primarily upon whether the species can develop any efficient means to attain nearly complete avoidance of mating or reproductive disturbance between each other.

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生殖干渉による競争排除

久　野　英　二

同じ生態的ニッチを持つ複数種は共存できないとする「競争排除則」が昆虫，特に植食性昆虫の世界では一般に成立しないことは現在ではよく知られ，その理論的根拠も示されている．しかし，一方，ごく近縁な種の間では，明瞭な空間的ないし時間的な「すみわけ」現象がしばしば見られることも事実であり，この現象を従来の資源をめぐる競争，つまり Volterra の競争方程式の文脈内で説明することはむずかしい．この研究では種間相互作用の機構として生殖（交尾）干渉を想定し，Volterra 型の単純な微分方程式を作成してこのような「すみわけ」の説明を試みた．このモデルでは，資源競争モデルとの対比において，(1) どんなパラメータ条件下でも競争結果は確定的ではなく，初期条件しだいでどちらの種が勝つ場合もありうること，および (2) 同一パラメータ条件下では安定共存の可能性がはるかに限定されることが示された．この結果から，生殖干渉は，資源の取り合いが競争機構として有効に働かない野外昆虫群集においても，競争排除をひきおこす機構として現実に機能している可能性が高いと考えられる．