omplex organisms
apparently recent
of the molecular
does this relate to
in Fig. 1)?

ociated with British

l flies on the British

62, 67–73.
eir associated insect

rees. *J. anim. Ecol.*

sects and their host

h trees. *Proc. Natl.*

Evolutionary Ecology, 1987, **1**, 247–262

The evolution of competing species of terrestrial salamanders: niche partitioning or interference?

NELSON G. HAIRSTON Sr, KIISA C. NISHIKAWA* and SARAH L. STENHOUSE‡
Department of Biology, University of North Carolina, Chapel Hill, NC 27514, USA

Summary

One of the central assumptions of evolutionary ecology is that interspecific competition is a potent evolutionary force acting on coexisting species. There are few animal species that provide an opportunity for an experimental analysis of the evolutionary consequences of the phenomenon. We have taken advantage of the fact that two species of terrestrial salamander, *Plethodon glutinosus* and *P. jordani*, have different altitudinal distributions on two mountain ranges in North Carolina. Field removal experiments showed that interspecific competition was much stronger in the Great Smoky Mountains than in the Balsam Mountains, and transplant experiments between the two mountain ranges showed that neither species from the Balsam Mountains had a measurable effect on its congener in the Smokies, although both species from the Smokies had strong negative effects on the Balsam congeners. Other experiments were conducted on the behavioral and ecological changes that have (or have not) evolved in the two areas. Our studies show that increased interspecific interference was the major evolutionary response of these large *Plethodon* species to interspecific competition, and that partitioning of food or microhabitat was not involved.

Keywords: Aggression; altitudinal distribution; food interference; North Carolina; *Plethodon*; salamander.

Introduction

Theoretical development in evolutionary ecology has been based on the assumption that competition between species is a major factor. This assumption has received some confirmation from the large number of field experiments which have shown that competition is common in nature (Schoener, 1983; Connell, 1983). It is not, however, of universal occurrence. Some experimental tests for competition have yielded negative results (e.g. Hairston, 1981), and predation has been shown to be important in a number of communities (Paine, 1966; Connell, 1975; Hairston, 1986).

Several mathematical ecologists have concluded that the evolutionary consequence of interspecific competition is the adaptation of competing species to different but overlapping parts of the resource for which they are assumed to compete (MacArthur and Levins, 1967; MacArthur, 1972; Roughgarden, 1976; Lawlor and Maynard Smith, 1976; Pianka, 1976). Because one can always find ecological differences between coexisting species (Wiens, 1977), the mathematical theories have been widely regarded as confirmed. Despite this apparently neat package of theory, observation and experiment, there has been an alternative hypothesis in the literature for 13 years. In 1974, D. E. Gill proposed that rather than the partitioning of resources, a likely outcome of interspecific competition is the evolution of interference mechanisms, by which one species is able to reduce the ability of a competing species to obtain a resource, or to survive or

---

* Now at School of Biological Sciences, University of Kentucky, Lexington KY40506–0225.
‡ Now at 424 Bertonly Ave., Charlotte, NC 28211, USA.

0269–7653/87 $03.00+.12

reproduce. Gill's example was the use of symbiotic microorganisms by *Paramecium* to produce substances lethal to potential competitors, and there are other good examples, such as the production of antibiotics by the fungi that compete with bacteria in decomposition. The ecological effect of interference, as opposed to exploitation, has been considered by modelers (Case and Gilpin, 1974; Schoener, 1976, 1978), but the relative importance of the two in evolutionary terms has not received mathematical attention.

We have taken advantage of a unique opportunity to study the evolutionary consequences of interspecific competition in two species of terrestrial salamander, *Plethodon jordani* and *P. glutinosus*. These species are unique in exhibiting geographic variation in the intensity of interspecific competition. Our studies describe the observational and experimental evidence for the difference in strength of competition on different mountain ranges, the use of food and microhabitat by the two species, and test alternative hypotheses for the behavioral basis of the difference.

Plethodon jordani is a salamander species endemic to the southern Appalachians, with many populations isolated or partially isolated on different mountain ranges (Dunn, 1926; Hairston, 1951; Highton and Henry, 1970). Some of these forms differ strikingly in color pattern. For example, *P. jordani* in the Great Smoky Mountains of North Carolina and Tennessee have red cheeks, while those in the Balsam Mountains of North Carolina have grey cheeks. The two populations intergrade freely where the two mountain ranges come together.

Plethodon glutinosus consists of regionally differing populations occurring at lower elevations throughout the eastern United States (Highton, 1972, 1983). The form in that part of the southern Appalachians concerned in these studies has been called *P. teyahallee* by Highton (1983), but the evidence for its specific distinctness from most surrounding forms is lacking, and we continue to use the name *glutinosus*. All members of the genus *Plethodon* are completely terrestrial, the eggs being laid underground, with metamorphosis taking place before hatching. Thus, there is no annual migration, and a complex life cycle is lacking.

Altitude distributions and field experiments

The altitudinal distribution of the two species differs among mountain ranges (Hairston, 1951). *Plethodon jordani*, a montane species, is found to the tops of all of the mountains, and *P. glutinosus* is found at lower elevations. In the Black Mountains of North Carolina and in the Great Smoky Mountains of North Carolina and Tennessee, the high-altitude *P. jordani* and the low-altitude *P. glutinosus* overlap by no more than 70–170 m vertically. The actual elevation of the overlap depends on the direction in which the slope faces — about 900 m on north-facing slopes and about 1500 m on south-facing ones. This distribution pattern of altitudinal replacement was originally interpreted as indicating strong competition between the species, as there is no discernable break in soil type or vegetation, and the climate changes gradually with altitude (Hairston, 1949).

In the Balsam Mountains of North Carolina, which are located between the Blacks and the Smokies, the altitudinal overlap between the two species is at least 1350 m (Hairston, 1951; Table 1). Although the *P. jordani* in the Smokies and Balsams differ in color and in some morphological characters (Hairston and Pope, 1948), the populations are distributed continuously, and the characters intergrade freely where the mountain ranges join. The discovery of this distribution pattern of broad altitudinal sympatry in the Balsams meant that, if the original interpretation of intense competition in areas of narrow altitudinal overlap was correct, the intensity of competition must differ among mountain ranges, being much stronger where the overlap was narrow than where it was wide.

Table 1. Altitudi
number of specime
trips.

	Great
Elevation (m)	No. *P. jorc*
*1622	241
1586	29
*1512	268
*1463	330
*1433	327
*1406	210
1372	6
*1348	0
1311	0
1265	1
1204	0
960	0

An experimen
was published in
1973). Briefly, it
same altitude in b
that had been o
strongly and mo
Balsams, becaus

The experime
(Highton, 1962).
levels of compet
jordani was rem
mean numbers o
In the Balsams,
through to the fi
populations of *P.*
two youngest ag
impressive incre
tion was confirm
there, as expecte

The numerical
capacities of the
specific competi

Table 1. Altitudinal transects in the Great Smoky Mountains and the Balsam Mountains, showing the number of specimens of *Plethodon* observed at each elevation. Asterisks indicate regular stops on class field trips.

Great Smoky Mountains				Balsam Mountains		
Elevation (m)	No. *P. jordani*	No. *P. glutinosus*	No. hybrids	Elevation (m)	No. *P. jordani*	No. *P. glutinosus*
*1622	241	0	0	1676	26	0
1586	29	0	0	1615	7	1
*1512	268	0	0	1525	16	7
*1463	330	0	0	1385	8	2
*1433	327	1	0	1240	11	6
*1406	210	70	4	1155	6	4
1372	6	3	0	1100	5	8
*1348	0	192	0	1051	3182	392
1311	0	23	0	1000	13	1
1265	1	37	0	915	6	2
1204	0	36	0	833	8	2
960	0	15	0	750	3	0
				560	10	0
				400	9	2
				250	3	8

An experimental test of the difference in intensity of competition was proposed, and the design was published in detail, along with the interpretations of different possible outcomes (Hairston, 1973). Briefly, it was proposed to remove each species from different experimental plots at the same altitude in both the Great Smoky Mountains and the Balsam Mountains. If the explanations that had been offered for the distributions were correct, each species should respond more strongly and more quickly to the removal of the other in the Smokies than they would in the Balsams, because of the hypothesized greater importance of competition in the former location.

The experiment ran for five years, the minimum duration of a generation of *P. glutinosus* (Highton, 1962). The results were similar to those expected under the hypothesis of different levels of competition in the two mountain ranges (Hairston, 1980a). On plots from which *P. jordani* was removed in the Smokies, mean numbers of *P. glutinosus* rose significantly above mean numbers on control plots during the third, fourth, and fifth years of the experiment (Fig. 1). In the Balsams, the same response was obtained, but only from the end of the fourth year through to the fifth (Fig. 2). Removal of *P. glutinosus* resulted in non-significant increases in the populations of *P. jordani*, but produced a marked and significant increase in the proportion of the two youngest age classes of *P. jordani* in the Smokies, and a statistically significant, but less impressive increase in these young animals in the Balsams. Thus, although interspecific competition was confirmed in both areas, it was detected earlier in the Smokies, and was more intense there, as expected from the altitudinal distributions.

The numerical results were used to calculate the coefficients of competition and the carrying capacities of the environments, assuming that the familiar Lotka–Volterra equations for interspecific competition were valid. The results are shown in Table 2. Each coefficient, alpha,

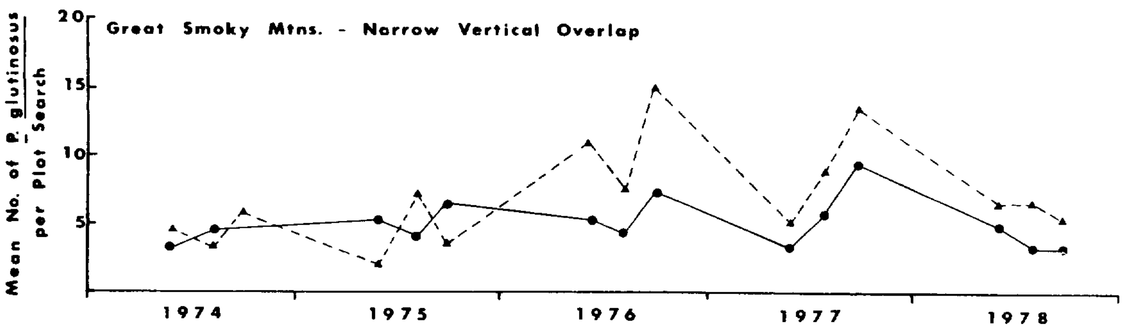


Figure 1. The effect of removing *Plethodon jordani* on the mean number of *Plethodon glutinosus* per plot search in the Great Smoky Mountains. (From 'The experimental test of an analysis of field distributions' by N. G. Hairston, *Ecology* **61**, 817–26. © 1980 Ecological Society of America. Reprinted by permission.)

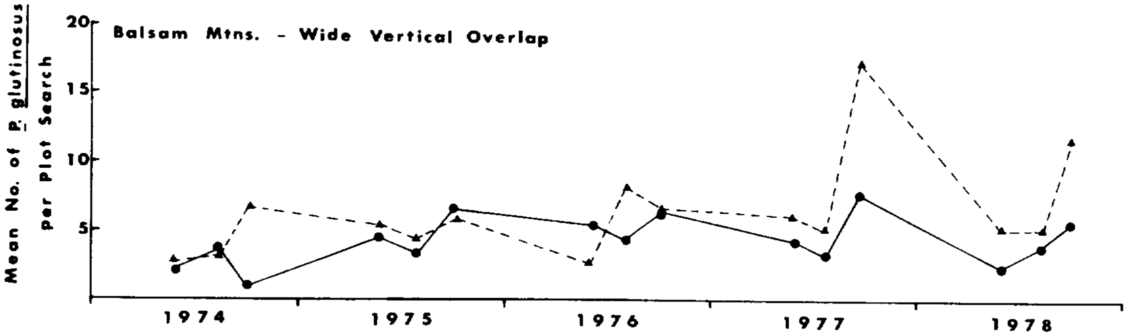


Figure 2. The effect of removing *Plethodon jordani* on the mean number of *Plethodon glutinosus* per plot search in the Balsam Mountains. (From Hairston, as Fig. 1)

Table 2. Coefficients of competition between *Plethodon jordani* and *Plethodon glutinosus* in two mountain ranges in North Carolina. Their calculation depends on the assumptions that populations are in equilibrium and that there is a linear relationship between the abundance of one competitor and the negative effect on the population of the other. Thus, the reduction of an average of 18 *P. jordani* resulted in an average increase of 3.52 *P. glutinosus*. The effect per individual *P. jordani*, 3.52/18, or 0.19, is the competition coefficient $\alpha_{g,j}$; Hairston (1983b) provides evidence of an equilibrium population of *P. jordani*. The same assumptions are necessary for the calculation of the carrying capacities (K) of the respective environments.

	Great Smoky Mountains (altitudinal overlap narrow)	Balsam Mountains (altitudinal overlap wide)
Competition coefficients:		
$\alpha_{g,j}$	0.19	0.14
$\alpha_{j,g}$	2.26	0.63
Carrying capacities:		
K_j	45.27	47.43
K_g	11.69	10.93

represents the nu
added to its popu
Smoky Mountain
the removal of a
capacities repres
environment in t
two mountain ra
standpoint of sui

The establishn
altitudinal distrit
tions of each sp
ecological situati
an intermediate
harbors the ance

Both of the alt
in the intensity c
ence mechanism
areas meant that
the introduced
increased compe
of *jordani* from t
the local *glutin*
specifically evol
evolved in the I
would have diffe
result in an impr
it would be re
partitioning had
and thus have le
the ability of the
competition. A
from the distan
measure the eff

The results c
Smoky Mounta
Mountains resu
the controls; in
significant incre
these experime

The effect o
Balsams was tw
Balsams *jordar*
effective agains
Neither species
Smokies, even
resource partit
then Balsams
Smokies. That

represents the number of individuals of the species designated by the first subscript that could be added to its population by the removal of one individual of the second species. Thus, in the Great Smoky Mountains, removal of one *P. glutinosus* would result in the addition of 2.26 *jordani*, and the removal of about five *jordani* would result in the addition of one *glutinosus*. The carrying capacities represent the calculated number of each species that could be supported by each environment in the absence of the other species. The similarity of the carrying capacities on the two mountain ranges shows that the locations chosen for the experiments were similar from the standpoint of suitability for both species.

The establishment of differences in intensity of competition as the reason for the different altitudinal distributions poses an evolutionary question. Assuming that the respective populations of each species share common ancestors in the geologically recent past, one of the two ecological situations was probably derived from the other, or both could have been derived from an intermediate state. There is no distributional or other evidence as to which mountain range harbors the ancestral ecological relationship.

Both of the alternative hypotheses described above could account for the observed differences in the intensity of competition. Either resource partitioning evolved in the Balsams, or interference mechanisms evolved in the Smokies. The differing color pattern of *P. jordani* in the two areas meant that populations could be substituted between the mountain ranges and the fate of the introduced forms, and of the *glutinosus* newly exposed to them, could be followed. If increased competitive ability had evolved in the Smokies, substituting a red-cheeked population of *jordani* from there for the grey-cheeked form on plots in the Balsams should be detrimental to the local *glutinosus* population, which would thus be exposed to a group of salamanders specifically evolved to compete better with it. If, on the other hand, resource partitioning had evolved in the Balsams, the effect of the substitution on *glutinosus* should be minimal, since it would have different requirements from the introduced form. The reciprocal substitution should result in an improved situation for *glutinosus*, because if interference had evolved in the Smokies, it would be relieved of the extra competitive ability of the local *jordani*; and if resource partitioning had evolved in the Balsams, the introduced form should have different requirements, and thus have less negative influence. These experiments required extra control plots, to confirm the ability of the introduced forms to survive and reproduce in the new location in the absence of competition. Accordingly, both species were removed from two plots in each area, and *jordani* from the distant location were introduced. A by-product of these controls was the ability to measure the effect of the local *glutinosus* on the introduced *jordani*.

The results confirmed the hypothesis that interference competition has evolved in the Great Smoky Mountains (Hairston, 1980b; 1983a). Introducing red-cheeked *jordani* into the Balsam Mountains resulted in a statistically significant decrease in the number of *glutinosus*, relative to the controls; introducing grey-cheeked *jordani* into the Great Smoky Mountains resulted in a significant increase in the number of *glutinosus*. The competition coefficients calculated from these experiments are given in Table 3.

The effect of the highly competitive *P. jordani* from the Smokies on *P. glutinosus* in the Balsams was twice as great as on its coevolved *glutinosus*, and three times as great as the effect of Balsams *jordani* on its local *glutinosus*. *P. glutinosus* in the Smokies was appreciably more effective against the introduced *jordani* than the Balsams *glutinosus* was against the same form. Neither species from the Balsams had any appreciable effect on the opposite species from the Smokies, even though they had been shown to compete with each other, as shown in Table 2. If resource partitioning were responsible for the smaller competition coefficients in the Balsams, then Balsams salamanders should have had a measurable effect on populations from the Smokies. That they did not is additional evidence in favor of the evolution of specific interference

Table 3. Coefficients of competition between *Plethodon jordani* and *P. glutinosus* for combinations between the two areas where competition is strong and weak, respectively.

	Smokies *jordani* vs Balsams *glutinosus*	Balsams *jordani* vs Smokies *glutinosus*
$\alpha_{g.j}$	0.40	0.03
$\alpha_{j.g}$	0.00	0.87

mechanisms in both species in the Smokies, and against the evolution of resource partitioning in the Balsams.

The search for a limiting resource: an indirect test for food competition

The resource most commonly assumed to be in limited supply is food, and most plethodontid salamanders, including *P. jordani* and *P. glutinosus*, qualify as potential competitors for food, since they are generalist predators feeding on any moving organism of an appropriate size. In addition to the experimental species in the previous studies, four or five other terrestrial species of plethodontids were observed on the plots. All of them overlap broadly in diet with *P. jordani* and *P. glutinosus* (Hamilton, 1932; Jameson, 1944; Hairston, 1949; Davidson, 1956; Whitaker and Rubin, 1971; Powders and Tietjen, 1974; Burton, 1976). If food is a limiting resource in communities of these animals, removal of either of those two species (respectively 40–50% and 10% of the total salamander biomass on the plots) should have had a favorable effect on the abundances of the other species. There was no evidence for competitive release of any of the remaining five species of salamander following removal of either *P. jordani* or *P. glutinosus* (Hairston, 1981). The abundance of *Plethodon serratus*, the species most like the two experimental ones, did not differ significantly on removal vs control plots in either the Balsam Mountains or the Great Smoky Mountains, and the results were similar for the other plethodontid species (*Desmognathus ochrophaeus*, *D. wrighti*, *D. imitator* and *Eurycea bislineata*). Significant differences in density between control and removal plots were found only as frequently as expected by chance. We conclude that food does not limit the populations of this group of species. These results also imply that *P. jordani* and *P. glutinosus* do not compete for food. If they did, the shared resource would be much more abundant after the removal of one of them, and thus should have benefited the remaining members of the plethodontid community.

Direct tests for niche-partitioning

The observed geographic variation in the intensity of interspecific competition, measured by the removal experiments, formed the basis for several studies that attempted to relate the degree of niche overlap between *P. jordani* and *P. glutinosus* to the intensity of competition in the two areas. The general form of the hypothesis tested in these studies is that the species should differ more in resource use in the Balsam Mountains, where competition is weaker, than they do in the Great Smoky Mountains, where competition is more intense. Confirmation of this hypothesis would give strong support for the theory that resource partitioning is the dominant evolutionary response to interspecific competition. Of course, if the availability of different parts of the resource differed greatly between the areas, the test would not be valid. However, that would be

---

an assumption ir
as well as their
capacities (Tabl
species, and the
microhabitats. T
Timing of activit
the two species,

These two spe
of the ground.
various plants. S
September, whe
to be obtaining
partitioning.

To test the a
competition is l
different nights
contents were o
diet in each are
Siegel, 1956) fo
species, and the
in the stomach c

Figure 3. The d
and *P. glutinosus*
(A) and the Grea
Balsam Mountains
nosus stomachs a
Great Smoky Mou
glutinosus stoma
stomachs.

an assumption in violation of the obvious similarity between the two areas, as shown by the biota, as well as their suitability for the two species of *Plethodon*, as shown by the similar carrying capacities (Table 2). No single resource has yet been identified as a limiting factor for either species, and therefore two commonly partitioned resources were analyzed: food and foraging microhabitats. There is no evidence that the salamanders partition their use of resources in time. Timing of activity, both diel (they are nocturnal) and seasonal (May–October), is very similar in the two species, as confirmed repeatedly during the removal experiments.

These two species are active only at night, when they come out from retreats below the surface of the ground. On some humid, foggy nights many individuals can be observed climbing on various plants. Sometimes, the entire active population appears to do so. Except in August and September, when adults can be found mating, the purpose of this above-ground activity appears to be obtaining food, and therefore location could be an important element in any resource partitioning.

To test the above hypothesis that differences in diet are greater in the Balsams, where competition is less intense, than in the Smokies, specimens of both species were collected on different nights in both areas between nightfall and 0100 h, when activity declines. Stomach contents were obtained by pumping out the salamanders' stomachs (Fraser, 1976). Similarity of diet in each area (Fig. 3) was analyzed in two ways: a non-parametric test (Kendall's tau, see Siegel, 1956) for a correlation between the frequencies of prey items in the diets of the two species, and the overlap index: $\theta = 1 - 0.5 \sum |P_{ih} - P_{ij}|$, where P is the proportion of prey taxon i in the stomach contents of species h or j. This index has a value of 1.0 when diets are identical

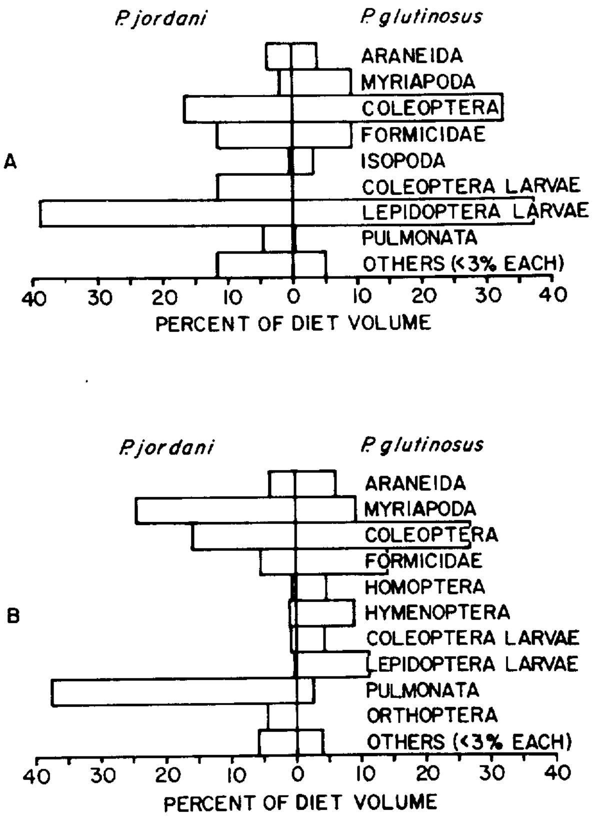


Figure 3. The diets of *Plethodon jordani* and *P. glutinosus* in the Balsam Mountains (A) and the Great Smoky Mountains (B). Balsam Mountains data: contents of 24 *glutinosus* stomachs and 51 *jordani* stomachs; Great Smoky Mountains data: contents of 42 *glutinosus* stomachs and 40 *jordani* stomachs.

and 0 when no items are consumed in common. Kendall's tau was 0.389 in the Balsams and 0.055 in the Smokies, the null hypothesis being that the selection of prey by the two species was independent. In neither area was there a significant correlation between the diets, but the similarity was greater in the Balsams, contrary to the hypothesis being tested. Similarly, θ in the Balsams was 0.721 and 0.442 in the Smokies. Again, the difference is in the wrong direction for the hypothesis that food has been partitioned where competition has been found to be weaker.

As the position of each salamander collected was recorded, the species could be compared for foraging microhabitats. There was no significant difference between the species in the overall proportions found climbing at either location. This varied on different nights from 0 to 0.65 in the Smokies and from 0.04 to 0.87 in the Balsams (species pooled for each area). The difference between areas is probably spurious, as the reverse was observed during the removal experiments. It is likely that observations were made on wetter nights in the Balsams in this particular study, and in the Smokies during the removal experiments. *Plethodon glutinosus* was found climbing significantly more on woody vegetation and *P. jordani* on herbaceous plants, a difference related to the relative sizes of the two species. The larger *glutinosus* is better supported on shrubs and trees than on herbs.

If natural selection had increased the amount of partitioning of microhabitats, we should expect greater differences between the behavior of the two species within the narrow zone of overlap where competition is strong than above the zone (*P. jordani*) or below it (*P. glutinosus*). The reverse was true. Within the zone of altitudinal overlap, 16 of 148 *glutinosus* (0.11) and 19 of 132 *jordani* (0.14) were climbing. The difference is not statistically significant. Above the overlap, 11 of 66 *jordani* (0.17) and below the overlap 0 of 109 *glutinosus* were climbing. Thus, the two species were more alike where they occurred together than where they were alone, in direct contradiction to the hypothesis of microhabitat partitioning.

Neither food nor microhabitat gave any evidence of being a resource that has been partitioned or is being partitioned between the two competing species. It is worth reporting that when Stenhouse began this work, she expected to find evidence of resource partitioning, using the approach that she took. Since the results of the reciprocal transplant experiments were not complete, it was a reasonable expectation, based on the dominant theory of community organization. The outcome of her study was consistent with the experimental manipulation, and some basis other than resource partitioning was sought for the relationship between *Plethodon jordani* and *P. glutinosus*.

Selection for competitive ability: the behavioral basis of alpha selection

The studies described above tested predictions of the hypothesis that differences between populations from the Balsam and Great Smoky Mountains in the intensity of competition are due to the evolution of niche differences between species in the Balsam Mountains populations, but not in those in the Great Smoky Mountains. The alternative hypothesis is that the intensity of competition has increased in the Smokies by the process of alpha selection (Hairston, 1980b, 1983a). In evolutionary ecology, the terms r selection and K selection are well known, r selection referring to the process whereby species become adapted to uncertain environments in which it is advantageous for a genotype to be able to increase in abundance rapidly, and K selection referring to the process whereby species become adapted to environments that are in some sense 'saturated', in which the ability of a genotype to take and retain limited resources is favored (MacArthur and Wilson, 1967). As described above, the term alpha selection was added later to designate the evolution of interference mechanisms (e.g. aggressive behavior or allelopathy) against competing species.

There is mucl
mediated throug
al., 1983; Jaeger
individual marks
attacks intruders
investigations. T
not especially se

Two sets of
interspecific inte
in the salamand
(Nishikawa, 198
of the two speci
conditions. For
that already hel
for 45 min. Fou
Snap and Bite.
significance are
acts were analyz

Geographic vari

In the first set o
Balsam and Gr
exhibited by *P.*
jordani are sho
cantly more agg

Figure 4. Avera
aggressive behav
Plethodon glutin
Smokies and B
with sympatric *P*
specifics (lower).
unfilled bars = B
the figure repres
dent (head raise
Nishikawa, 1985.

ılsams and 0.055
two species was
e diets, but the
imilarly, θ in the
ong direction for
d to be weaker.
be compared for
es in the overall
m 0 to 0.65 in the
. The difference
val experiments.
particular study,
s found climbing
difference related
ed on shrubs and

itats, we should
e narrow zone of
t (*P. glutinosus*).
s (0.11) and 19 of
bove the overlap,
g. Thus, the two
alone, in direct

been partitioned
orting that when
ioning, using the
iments were not
mmunity organi-
lation, and some
Plethodon jordani

ferences between
mpetition are due
populations, but
t the intensity of
Hairston, 1980b,
nown, r selection
ents in which it is
and K selection
are in some sense
ources is favored
vas added later to
r or allelopathy)

There is much experimental evidence that intraspecific competition among salamanders is mediated through aggressive behavior (Jaeger, 1974, 1981; Jaeger and Gergits, 1979; Jaeger *et al.*, 1983; Jaeger *et al.*, 1986). *Plethodon cinereus* has the attributes of territoriality, in that an individual marks an area with cloacal secretions, recognizes its own and those of others, and attacks intruders. Like *P. cinereus*, *P. jordani* and *P. glutinosus* are tractable for laboratory investigations. They carry out their behaviorial repertory within a relatively small space, and are not especially sensitive to human observers.

Two sets of experiments were undertaken to test the hypothesis that alpha selection for interspecific interference has occurred in the salamanders in the Great Smoky Mountains, but not in the salamanders in the Balsam Mountains, and to determine the mechanism of interference (Nishikawa, 1985, 1987). In these experiments, intraspecific and interspecific aggressive behavior of the two species from both areas were compared in laboratory arenas under standardized test conditions. For each observation, a salamander was introduced into a circular plastic container that already held a resident individual of the same sex. The behavior of the resident was watched for 45 min. Four different kinds of behavior pattern were classified as aggressive: Chase, Lunge, Snap and Bite. These are shown separately in Figures 4–9, but statements about statistical significance are based on Principal Components Analysis, in which the frequencies of aggressive acts were analyzed simultaneously.

Geographic variation in aggressive behavior

In the first set of experiments, aggressive behavior was compared between salamanders from the Balsam and Great Smoky Mountains. The mean frequencies of aggressive behavior patterns exhibited by *P. glutinosus* from the two mountain ranges during encounters with sympatric *P. jordani* are shown in Fig. 4. Overall, *glutinosus* from the Great Smoky Mountains were significantly more aggressive toward sympatric heterospecifics than were those of Balsam Mountains

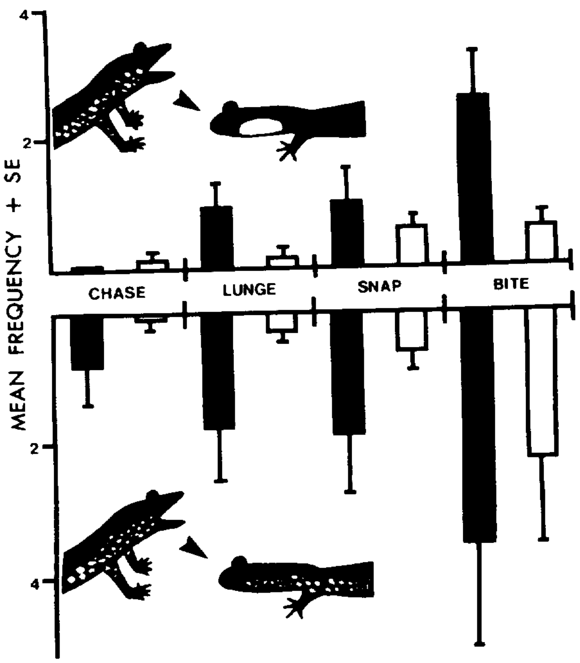


Figure 4. Average frequency (+ 1 SE) of aggressive behavior patterns exhibited by *Plethodon glutinosus* residents from the Smokies and Balsams during encounters with sympatric *P. jordani* (upper) and conspecifics (lower). Filled bars = Smokies; unfilled bars = Balsams. The salamanders in the figure represent the species of the resident (head raised) and the intruder. (From Nishikawa, 1985.)

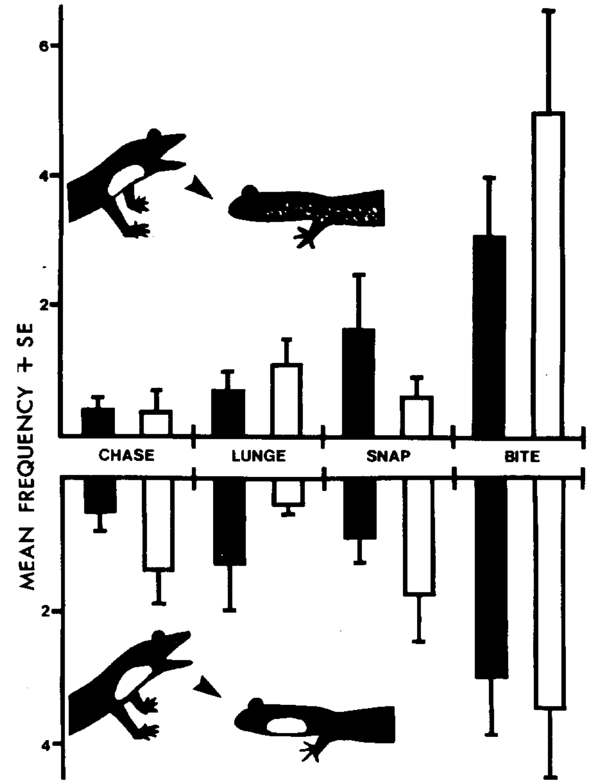


Figure 5. Average frequency (+ 1 SE) of aggressive behavior patterns exhibited by *Plethodon jordani* residents from the Smokies and Balsams during encounters with sympatric *P. glutinosus* (upper) and conspecifics (lower). Symbols and salamanders as in Fig. 4. (From Nishikawa, 1985.)

origin. No significant differences were found in intraspecific aggressive behavior between the two populations. The same was true of non-aggressive behavior patterns when intruders were absent.

The interspecific aggression of *P. glutinosus* supports the hypothesis that interference has evolved in the Great Smoky Mountains. The greater demographic effects of Smokies *glutinosus* on sympatric *jordani*, as well as on *jordani* transplanted from the Balsams (Table 3), appears to be the result of more frequent interspecific interference behavior by Smokies *glutinosus*. Furthermore, the more moderate aggressiveness of Balsams *glutinosus* toward heterospecifics can account for the lack of measurable impact of this form on the Smokies *jordani* that were transferred to the Balsams.

Aggressive behavior differed less between the populations of *P. jordani* than between the populations of *P. glutinosus* (Fig. 5). No significant difference was found between the populations in overall aggressiveness toward sympatric individuals of either species. This result might be expected on the basis of the relatively small difference in the estimated competitive effects of *jordani* on *glutinosus* in the two areas.

Species-specific interference

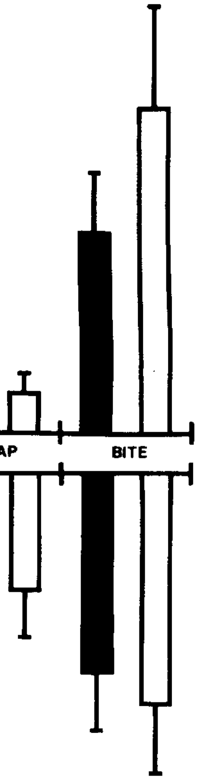
In the second set of experiments, for each species, interspecific aggression was compared with intraspecific aggression within mountain ranges to test whether or not the aggression exhibited by salamanders is species-specific. The experimental technique was the same as for the first set of experiments, as described above. Each resident was observed during an encounter with a sympatric heterospecific and with a sympatric conspecific intruder presented in random sequence

---

Figure 6. Averag
aggressive behavi
from the Bals
encounters with
(unfilled bars) a
bars).

at two-day inte
from the Balsam
Fig. 6. A signific
jordani from the
were towards co
relatively more
P. glutinosus, n
conspecifics and
Smokies, the in
greater than in

Figure 7. Avera
aggressive behav
from the Great
encounters wit
(unfilled bars)
bars).



between the two
ers were absent.
interference has
okies *glutinosus*
le 3), appears to
inosus. Further-
erospecifics can
rdani that were

an between the
the populations
result might be
etitive effects of

compared with
ion exhibited by
r the first set of
counter with a
ndom sequence

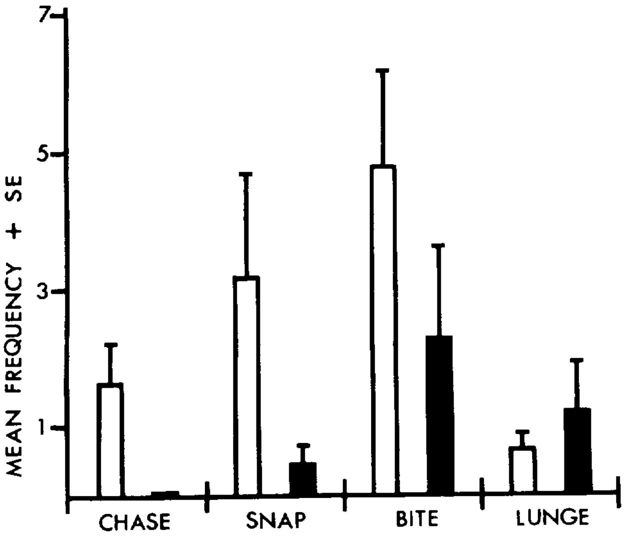


Figure 6. Average frequencies (+ 1 SE) of aggressive behavior patterns of *P. jordani* from the Balsam Mountains during encounters with sympatric conspecifics (unfilled bars) and heterospecifics (filled bars).

at two-day intervals. The frequencies of aggressive behavior patterns exhibited by *P. jordani* from the Balsam Mountains during encounters with conspecifics and heterospecifics are shown in Fig. 6. A significantly greater frequency of aggression was directed at conspecifics. In contrast, *P. jordani* from the Great Smoky Mountains were more aggressive towards *P. glutinosus* than they were towards conspecifics, although not significantly so (Fig. 7). Thus, as expected, *jordani* were relatively more aggressive to heterospecific competitors in the Smokies than in the Balsams. For *P. glutinosus*, no statistically significant differences were obtained between aggression toward conspecifics and heterospecifics, either in the Balsams (Fig. 8) or in the Smokies (Fig. 9). In the Smokies, the intensity of aggression of *glutinosus* toward all intruders, regardless of species, is greater than in the Balsams.

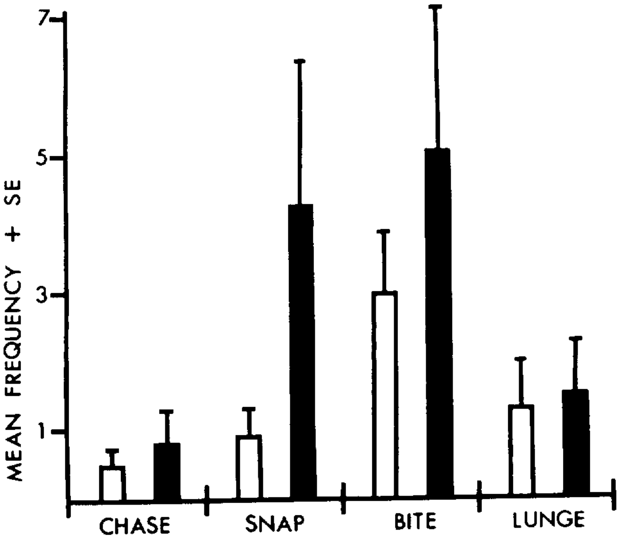


Figure 7. Average frequencies (+ 1 SE) of aggressive behavior patterns of *P. jordani* from the Great Smoky Mountains during encounters with sympatric conspecifics (unfilled bars) and heterospecifics (filled bars).

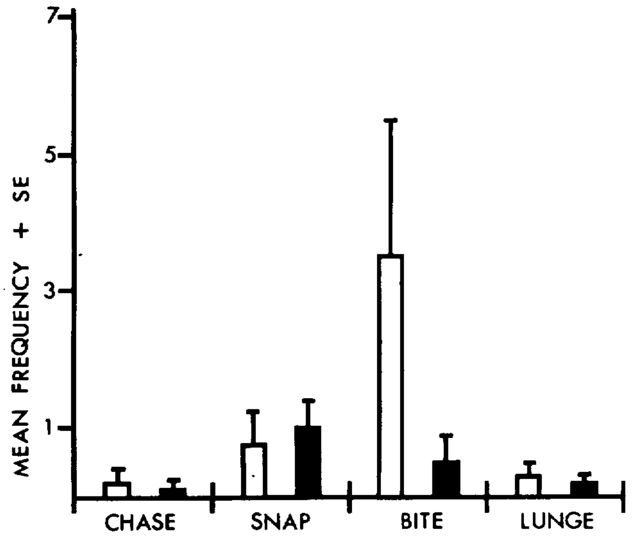


Figure 8. Average frequencies (+ 1 SE) of aggressive behavior patterns of *P. glutinosus* from the Balsam Mountains during encounters with conspecifics (unfilled bars) and heterospecifics (filled bars).

The results of the two sets of experiments, while they are not symmetrical between areas or between species, are consistently in favor of the hypothesis that interspecific aggression has increased in the Great Smoky Mountains. *Plethodon glutinosus* was significantly more aggressive toward *P. jordani* there than in the Balsam Mountains, and *P. jordani* was less aggressive toward *P. glutinosus* in the Balsams than it was toward members of its own species, a result not obtained on individuals from the Smokies.

The difference in the pattern of variation in aggressive behavior between species appears to be related to differences in population density and relative abundance. *P. jordani* is found at higher densities than *P. glutinosus* throughout its range in the southern Appalachians, and intraspecific aggression has been observed in several different populations (Organ, 1958; Hutchison, 1959;

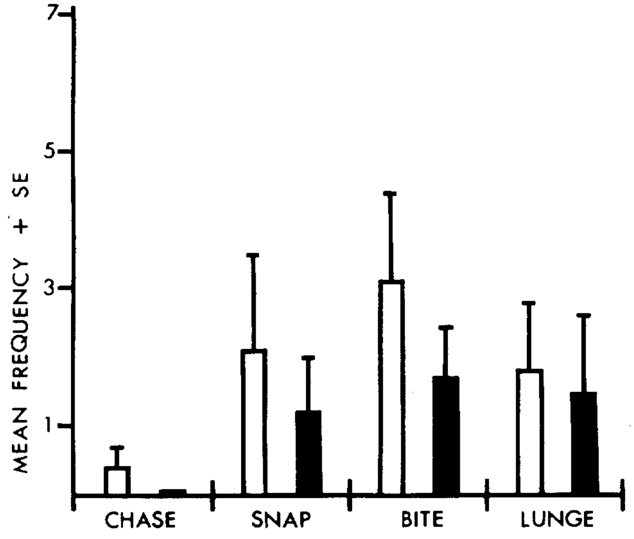


Figure 9. Average frequencies (+ 1 SE) of aggressive behavior patterns of *P. glutinosus* from the Great Smoky Mountains during encounters with conspecifics (unfilled bars) and heterospecifics (filled bars).

Arnold, 1976).
elsewhere, *P. j*
intraspecific co
Great Smoky
interspecific ag
the stronger in
In contrast,
out the southe
with that speci
much as six or
glutinosus shou
In the Great S
species, than i
the more inten

Conclusions

We have accun
tion, the inten
intensity of int
salamander in
data form a c
about the evol
competition.

Two contras
course of evol
lines of evide
hypothesis tha
competition, a
interference m

(1) In trans
some effect on
tion between t
level there, the
absence of inte
Smokies indica

(2) In the re
validity of the
tion, they sho
competition co

(3) The five
glutinosus sho
supply in this c

(4) While *P.*
actually less in
evidence again
as to partition

(5) Foraging

Arnold, 1976). In the Balsam Mountains, where interspecific competition is less severe than elsewhere, *P. jordani* is more aggressive to conspecifics than to heterospecifics. This is expected if intraspecific competition is relatively more intense than interspecific competition there. In the Great Smoky Mountains, alpha selection has brought about an increase in the frequency of interspecific aggression relative to the frequency of intraspecific aggression, and this is reflected in the stronger interspecific competition there (Table 2).

In contrast, *Plethodon glutinosus* exists at lower population densities than *P. jordani* throughout the southern Appalachians, and aggression is only known in populations that are sympatric with that species. Where they occur together, *P. jordani* outnumbers its larger congener by as much as six or eight to one (Hairston, 1980a). In sympatry, individuals of the less abundant *P. glutinosus* should encounter *P. jordani* more frequently than they should conspecific individuals. In the Great Smoky Mountains, *glutinosus* was more aggressive to all intruders, regardless of species, than in the Balsam Mountains (Fig. 4), and that greater aggressiveness was reflected in the more intense competition in the Smokies.

Conclusions

We have accumulated evidence from eight sets of observations and experiments on the distribution, the intensity of interspecific competition, the use of food and microhabitats, and the intensity of intraspecific and interspecific aggressive behavior of two closely related species of salamander in the southern Appalachians. These distributional, demographic and behavioral data form a coherent, consistent body of information that allows us to draw firm conclusions about the evolution of *Plethodon jordani* and *P. glutinosus* under the influence of interspecific competition.

Two contrasting, but not mutually exclusive, hypotheses have been advanced to predict the course of evolution among competing species: niche partitioning and alpha selection. Several lines of evidence from our experiments contradict the prediction of the niche partitioning hypothesis that differential exploitation of limited resources will be the result of interspecific competition, and support the hypothesis that natural selection has favored the evolution of interference mechanisms:

(1) In transplant experiments, the Balsam Mountains salamanders were predicted to have some effect on those from the Great Smoky Mountains, because there was measurable competition between the two species in the Balsams. If competition had simply been reduced to a lower level there, they should still have had an effect on the heterospecifics from the Smokies. The total absence of interspecific competitive effects of Balsam Mountains salamanders on those from the Smokies indicates that competition occurs by interference rather than by exploitation.

(2) In the removal experiments, the competition coefficients, calculated on the assumption of validity of the Lotka–Volterra equations, are not reciprocal. With purely exploitative competition, they should be. This is further evidence for interference, which does not require the competition coefficients to be reciprocal.

(3) The five sympatric plethodontid species that share food resources with *P. jordani* and *P. glutinosus* showed no numerical response to their removal, suggesting that food is not in limited supply in this community.

(4) While *P. jordani* and *P. glutinosus* differed in diet in both areas, these differences were actually less in weakly competing populations than in strongly competing ones. This is important evidence against the hypothesis that in the area of weak competition, the species have evolved so as to partition the resource of food.

(5) Foraging microhabitats were not more different between weakly competing populations

than between strongly competing ones. Furthermore, foraging microhabitats were more alike in sympatric populations than in allopatric populations in the same mountain range.

(6) The behavioral experiments on interspecific aggression provide direct evidence that alpha selection for interspecific interference has occurred in the Great Smoky Mountains populations of both species. The more intense interspecific aggressive behavior of both species in the Great Smoky Mountains has resulted in stronger competition there, and has caused the exclusion of *P. jordani* from the lower elevations and the exclusion of *P. glutinosus* from the higher slopes, leaving a narrow zone of 70–170 m where they coexist; in contrast to the Balsam Mountains, where the two species coexist over a zone at least 1350 m wide.

For historical reasons, independent of competition, *P. jordani* is better adapted to the cool, moist conditions at the tops of the mountains; *P. glutinosus* can apparently withstand better the warmer, dryer conditions at the foot of the mountains. The level of competition, expressed as aggressive interference, determines the extent to which each species can exclude the other from intermediate elevations.

The concept of niche partitioning has a rich history, with a coherent mathematical theory and an impressive body of fact that is consistent with the theory in many details (Cody and Diamond, 1975; Hutchinson, 1978; Roughgarden, 1979). However, the coherence of the theory and the facts has been achieved at the cost of ignoring alternative hypotheses, and even of disregarding conflicting observations (Simberloff, 1978, 1983; Roth, 1981; Dayton, 1973). While interference competition has acquired a theoretical basis (Ayala, Gilpin and Ehrenfeld, 1973; Case and Gilpin, 1974; Schoener, 1976, 1978), it has not been worked into community theory and its absence constitutes a serious deficiency in the generality of that theory (Hairston, 1973, 1980b, 1983a). Schoener's recent review (Schoener, 1983) of field experiments on interspecific competition revealed that in 100 of 171 studies, some form of interference can be seen to play a role in competition. That is too large a proportion to be ignored.

In this case, and probably in others, interference competition has led to the superficial appearance of niche partitioning. However, the causes of the two phenomena, in terms of natural selection, are quite distinct. The present study permits a clear choice between the two responses to competition, and strongly supports selection for competitive ability.

Acknowledgements

The removal and transplant experiments (N.G.H.) were supported by the William R. Kenan Professorship Fund, University of North Carolina. The study of food habits and microhabitat distribution (S.L.S.) was supported by a grant in aid from the Highlands Biological Station. The behavior experiments (K.C.N.) were supported by grants in aid from the Highlands Biological Station. Earlier versions of the manuscript derived much benefit from the comments of R. K. Colwell, D. F. Fraser, N. G. Hairston Jr, P. M. Service, M. T. Southerland, M. Turelli, and D. B. Wake. We are also most grateful to family, friends and colleagues who gave much volunteer assistance with the field work.

References

Arnold, S. J. (1976) Sexual behavior, sexual interference and sexual defense in the salamanders *Ambystoma maculatum*, *Ambystoma tigrinum* and *Plethodon jordani*. *Z. Tierpsychol.* **42**, 247–300.

Ayala, F. J., Gilpin, M. E. and Ehrenfeld, J. G. (1973) Competition between species. Theoretical models and experimental tests. *Theor. Pop. Biol.* **4**, 331–56.

Burton, T. M. (1
Hubbard Br
Case, T. J. and C
71, 3073–7.
Cody, M. L. and
Press, USA.
Connell, J. H. (1
from field ex
eds) pp. 460
Connell, J. H. (1
field experin
Davidson, J. A.
Herpetologic
Dayton, P. K. (
prediction fo
Dunn, E. R. (19
Fraser, D. F. (19
Plethodon.
Gill, D. E. (1974
competitive
Hairston, N. G.
Appalachian
Hairston, N. G.
Appalachian
Hairston, N. G.
Hairston, N. G.
salamanders
Hairston, N. G
salamanders
Hairston, N. G.
Hairston, N. G.
hypothesis.
Hairston, N. G
selective pr
Hairston, N. G.
predation a
Hairston, N. G.
(*Plethodon*
Hamilton, W. J.
Highton, R. (19
Highton, R. (1
Plethodon.
138–88. Re
Highton, R. (1
southern A
Highton, R. a
salamander
Hutchison, V.
Hutchinson, G.
Jaeger, R. G.
J. Herp. **8**,
Jaeger, R. G.
Natur. **117**

re more alike in
e.
lence that alpha
s populations of
es in the Great
exclusion of P.
higher slopes,
am Mountains,

ted to the cool,
stand better the
n, expressed as
the other from

tical theory and
and Diamond,
theory and the
of disregarding
ile interference
1973; Case and
theory and its
n, 1973, 1980b,
pecific competi-
o play a role in

the superficial
erms of natural
two responses

iam R. Kenan
d microhabitat
al Station. The
nds Biological
nents of R. K.
Turelli, and D.
nuch volunteer

ers *Ambystoma*

oretical models

Burton, T. M. (1976) An analysis of the feeding ecology of the salamanders (Amphibia: Urodela) of the Hubbard Brook Experimental Forest, New Hampshire. *J. Herp.* **10**, 187–204.

Case, T. J. and Gilpin, M. E. (1974) Interference competition and niche theory. *Pr. Nat. Acad. Sci. (US)* **71**, 3073–7.

Cody, M. L. and Diamond, J. M. eds (1975) *Ecology and Evolution of Communities*. Harvard University Press, USA.

Connell, J. H. (1975) Some mechanisms producing structure in natural communities: a model and evidence from field experiments. In *Ecology and Evolution of Communities* (M. L. Cody and J. M. Diamond, eds) pp. 460–90. Harvard University Press, USA.

Connell, J. H. (1983) On the prevalence and relative importance of interspecific competition: evidence from field experiments. *Amer. Natur.* **122**, 661–96.

Davidson, J. A. (1956) Notes of the food habits of the slimy salamander *Plethodon glutinosus glutinosus*. *Herpetologica* **12**, 129–31.

Dayton, P. K. (1973) Two cases of resource partitioning in an intertidal community: making the right prediction for the wrong reason. *Amer. Natur.* **107**, 662–70.

Dunn, E. R. (1926) *The Salamanders of the Family Plethodontidae*. Smith College 50th Ann. Pubs.

Fraser, D. F. (1976) Empirical evaluation of the hypothesis of food competition in salamanders of the genus *Plethodon*. *Ecology* **57**, 459–71.

Gill, D. E. (1974) Intrinsic rate of increase, saturation density, and competitive ability. II. The evolution of competitive ability. *Amer. Natur.* **108**, 103–16.

Hairston, N. G. (1949) The local distribution and ecology of the plethodontid salamanders of the southern Appalachians. *Ecol. Monog.* **19**, 47–73.

Hairston, N. G. (1951) Interspecific competition and its probable influence upon the vertical distribution of Appalachian salamanders of the genus *Plethodon*. *Ecology* **32**, 266–74.

Hairston, N. G. (1973) Ecology, selection and systematics. *Breviora* **414**, 1–21.

Hairston, N. G. (1980a) The experimental test of an analysis of field distributions: competition in terrestrial salamanders. *Ecology* **61**, 817–26.

Hairston, N. G. (1980b) Evolution under interspecific competition. Field experiments on terrestrial salamanders. *Evolution* **34**, 409–20.

Hairston, N. G. (1981) An experimental test of a guild: salamander competition. *Ecology* **62**, 65–72.

Hairston, N. G. (1983a) Alpha selection in competing salamanders: experimental verification of an a priori hypothesis. *Amer. Natur.* **122**, 105–13.

Hairston, N. G. (1983b) Growth, survival and reproduction of *Plethodon jordani*: trade-offs between selective pressures. *Copeia* 1983, 1024–35.

Hairston, N. G. (1986) Species packing in *Desmognathus* salamanders: experimental demonstration of predation and competition. *Amer. Natur.* **127**, 266–91.

Hairston, N. G. and Pope, C. H. (1948) Geographic variation and speciation in Appalachian salamanders (*Plethodon jordani*) Group. *Evolution* **2**, 266–78.

Hamilton, W. J. (1932) The food and feeding habits of some eastern salamanders. *Copeia* 1932, 83–6.

Highton, R. (1962) Geographical variation in the life history of the slimy salamander. *Copeia* 1962, 597–613.

Highton, R. (1972) Distributional interactions among eastern North American salamanders of the genus *Plethodon*. In *The Distributional History of the Biota of the Southern Appalachians* (P. C. Holt, ed.) pp. 138–88. Res. Div. Monog. 4, Va. Poly. Inst. & State U.

Highton, R. (1983) A new species of woodland salamander of the *Plethodon glutinosus* group from the southern Appalachian Mountains. *Brimleyana* **9**, 1–20.

Highton, R. and Henry, S. A. (1970) Evolutionary interactions between species of North American salamanders of the genus *Plethodon*. *Evol. Biol.* **4**, 211–56.

Hutchison, V. H. (1959) Aggressive behavior in *Plethodon jordani*. *Copeia* 1959, 72–3.

Hutchinson, G. E. (1978) *An Introduction to Population Ecology*. Yale University Press, USA.

Jaeger, R. G. (1974) Interference or exploitation? A second look at competition between salamanders. *J. Herp.* **8**, 191–4.

Jaeger, R. G. (1981) Dear enemy recognition and the costs of aggression between salamanders. *Amer. Natur.* **117**, 962–74.

Jaeger, R. G. and Gergits, W. F. (1979) Intra- and interspecific communication in salamanders through chemical signals on the substrate. *Anim. Behav.* **27**, 150–6.

Jaeger, R. G., Nishikawa, K. C. and Barnard, D. E. (1983) Foraging tactics of a terrestrial salamander: costs of territorial defense. *Anim. Behav.* **31**, 191–8.

Jaeger, R. G., Goy, J., Tarver, M. and Marquez, C. E. (1986) Salamander territoriality: pheromonal markers as advertisement by males. *Anim. Behav.* **34**, 860–4.

Jameson, E. W. Jr (1944) Food of the red-backed salamander. *Copeia* 1944, 145–7.

Lawlor, L. R. and Maynard Smith, J. (1976) The coevolution and stability of competing species. *Amer. Natur.* **110**, 79–99.

MacArthur, R. H. (1972) *Geographical Ecology*. Harper & Row.

MacArthur, R. H. and Levins, R. (1967) The limiting similarity, convergence, and divergence of coexisting species. *Amer. Natur.* **101**, 377–85.

MacArthur, R. H. and Wilson, E. O. (1967) *The Theory of Island Biogeography*. Princeton University Press, USA.

Nishikawa, K. C. (1985) Competition and the evolution of aggressive behavior in two species of terrestrial salamanders. *Evolution* **39**, 1282–94.

Nishikawa, K. C. (1987) Interspecific aggressive behavior in salamanders: species-specific interference or misidentification? *Anim. Behav.* **35**, 263–70.

Organ, J. A. (1958) Courtship and spermatophore of *Plethodon jordani metcalfi*. *Copeia* 1958, 251–9.

Paine, R. T. (1966) Food web complexity and species diversity. *Amer. Natur.* **100**, 950–61.

Pianka, E. R. (1976) Competition and niche theory. In *Theoretical Ecology* (R. M. May, ed.) pp. 167–96. Sinauer.

Powders, V. N. and Tietjen, W. L. (1974) The comparative food habits of sympatric and allopatric salamanders, *Plethodon glutinosus* and *Plethodon jordani* in eastern Tennessee and adjacent areas. *Herpetologica* **30**, 167–75.

Roth, V. L. (1981) Constancy in the size ratios of sympatric species. *Am. Nat.* **118**, 394–404.

Roughgarden, J. (1976) Resource partitioning among competing species — a coevolutionary approach. *Theor. Pop. Biol.* **9**, 388–424.

Roughgarden, J. (1979) *Theory of Population Genetics and Evolutionary Ecology: An Introduction*. Macmillan.

Schoener, T. W. (1976) Alternatives to Lotka–Volterra competition: models of intermediate complexity. *Theor. Pop. Biol.* **10**, 309–33.

Schoener, T. W. (1978) Effects of density-restricted food encounter on some single-level competition models. *Theor. Pop. Biol.* **13**, 365–81.

Schoener, T. W. (1983) Field experiments on interspecific competition. *Amer. Natur.* **122**, 240–85.

Siegel, S. (1956) *Nonparametric Statistics*. McGraw-Hill Book Co.

Simberloff, D. (1978) Using island biogeographic distributions to determine if colonization is stochastic. *Amer. Natur.* **112**, 713–26.

Simberloff, D. (1983) Competition theory, hypothesis testing, and other community ecological buzzwords. *Amer. Natur.* **122**, 626–35.

Wiens, J. A. (1977) On competition and variable environments. *Amer. Sci.* **65**, 590–7.

Whitaker, J. O. Jr and Rubin, D. C. (1971) Food habits of *Plethodon jordani metcalfi* and *Plethodon jordani shermani* from North Carolina. *Herpetologica* **27**, 81–6.

Phenotyp

ROBERT FAG
School of Fisheries

Summary

When individual
genotypic differe
reproductive succ
for evolution of g
view of theoretic
location can evol
results to includ
evolutionarily sta
to phenotypic pl
adaptation to pl
maintenance of p
sexual reproducti

Keywords: Adap
reproduction; so

Introduction

Plastic phenoty

Phenotypic pla
1942; Mayr, 19
with cues avail
morphology, o
from its enviro
its environmen
greater than t
phenotypic pla
Watt, 1983; Pa
approach to ph
The time take
environmental
environment c
ing machinery
the benefits a
those that pr
constraints (e.
allow precise

0269–7653/87 $03.