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Detection of density dependence from annual censuses of bracken-feeding insects

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Summary. A variety of techniques were used to test for density dependence in 32 time series from bracken-feeding insects. Seventeen taxa (primarily species, but including some pooled data from two or more closely related species whose larvae could not be distinguished in frond surveys) occurred on an open site; a woodland site held 15 taxa. For series of 12 years, collected on the open habitat, direct density dependence was detected by one or more of the techniques in 10 (58.8%) of 17 taxa, compared to only 5 (33.3%) of 15 taxa with time series of 8 years in length from the woodland habitat. Delayed density dependence was detected in 6 cases for the open site and in no cases at the woodland site. Either direct or delayed density dependence was found in 13 (76.5%) of 17 taxa for the open site and 13 (86.7%) of the 15 taxa which occurred on both sites. Although these results suggest a high frequency of density dependence in the species making up the bracken insect community, results from individual tests were extremely variable. Density dependence was detected least often by Vickery and Nudds' (1984) test, and most frequently by Varley and Gradwell's (1960) test, although the latter is prone to high rates of detecting spurious density dependence. Direct density dependence was detected most frequently in taxa that were univoltine and did not have delayed diapause, i.e. in those taxa whose life-histories conform most closely to the assumptions of the models underlying the analyses. Delayed density dependence occurred more frequently in species with more complex life-histories at the open site (taxa that were either bivoltine or multivoltine, or had delayed diapause). The results are consistent with the view that that the bracken herbivore assemblage consists of populations which are independently regulated by density dependent processes, although the present analyses suggest that we cannot rely on these tests to firmly show whether density dependence is present or not in an individual time series of the lengths considered here.

Key words: Bracken – Insect populations – Density dependence – Delayed density dependence – Time series

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The community of insects exploiting bracken (*Pteridium aquilinum* (L.) Kuhn) is well defined (Lawton 1976, 1984a; Lawton and MacGarvin 1986). It is ideal for studies of community structure because it contains a sufficient, but not overwhelming, number of species and because of the short generation times of the majority of species, so that annual samples represent a more-or-less complete turnover of individuals. The assemblage is predictable in total annual abundance, relative population abundances and the sequence in which species enter the assemblage each year (Lawton and Gaston 1989). No studies have concentrated on the patterns of occurrence of density dependence in such a discrete community. Nor have searches for density dependence in time-series considered the effects of different life-history patterns on the ability of the various methods to detect density dependence. Different life-history patterns in the bracken-insect assemblage allow such analyses under otherwise similar environmental conditions.

Explorations of the detection of density dependence have previously been carried out on a variety of taxonomic groups, such as ducks (Vickery and Nudds 1984), parasitoids and their hosts (Stiling 1987) and aphids and moths (Hanski 1990; Woiwod and Hanski 1992); others have considered heterogeneous taxa (Gaston and Lawton 1987; Stiling 1988; Hassell et al. 1989; Vickery and Nudds 1991), including one study where delayed density dependence was also considered (Turchin 1990). In general, these studies have detected density dependence in about a half of the species considered. There is one major exception to this pattern, the study of Woiwod and Hanski (1992), which considered 5715 time series from British aphids and moths. This study detected density dependence at the 0.05 probability level in 69–81% of cases in aphids depending on the choice of test, and 29–56% of cases in moths. The frequency of detection of density dependence was positively correlated with the length of the time series for the three tests used; Bulmer's (1975) first test, the test of Pollard et al. (1987) and the regression of k-value against logarithmic abundance (Varley and Gradwell 1960). Furthermore, the occurrence of temporal trends reduced the frequency of detec-

Table 1. Species included in the study, together with information on the life-history stage(s) counted in the routine censuses, the pattern of generations within and between years ([a], below), and information on observed levels of attack by parasitoids ([b], below)

Species	Stage counted	Generation pattern	Parasitoids
Collembola			
Bourletiella viridescens Gisin	nymphs & adults	M	none
Diptera			
Chirosia albifrons Tiens	larval mines	U	yes
C. histricina Rond.	larval mines	M	yes
C. parvicornis (Zett.)	larval galls	M	yes
Dasineura filicina (Kieff.)	larval galls	M	yes
D. pteridicola (Kieff.)	larval galls	M	?
Phytoliriomyza spp.	larval mines	U (B?)	?
Hemiptera			
Ditropis pteridis (Spin.)	nymphs & adults	U	yes
Macrosiphum ptericolens Patch	nymphs & adults	M	?
Monalocoris filicis (L.)	nymphs & adults	U	?
Hymenoptera			
Aneugmenus spp.	larvae	U/DD	yes
Stromboceros delicatulus (Fall.)	larvae	U/DD	?
Strongylogaster lineata (Christ)	larvae	U/DD	?
Tenthredo ferruginea Schr.	larvae	U	yes
Tenthredo sp. 2	larvae	U?	?
Lepidoptera			
Olethreutes lacunana (D. & S.)	larvae	U(B)	?
Paltodora cytisella (Curt.)	larval mines	U	yes

[a] Pattern of annual generations classified as follows: U, univoltine, single generation per year. B, bivoltine, two generations per year (parentheses, partial second generation). M, multivoltine, two, and probably three generations in some years. U/DD, univoltine, but with a delayed diapause, so that a proportion of larvae pupating in year n delay emergence until year $n+2$, $n+3$ etc

[b] Laboratory rearing and observations in the field show that some species are regularly attacked by one or more species of parasitoids; these species have 'yes' in column 4. Parasitoids have never been recorded attacking species marked ? (although this does not mean that parasitoids are necessarily absent)

tion. If time series of less than 21 years and/or with trends were excluded, then density dependence was detected in 87–91% of time series for aphids and 67–88% for moths.

Intensive studies of the herbivores feeding on bracken have been carried out at Skipwith Common, in North Yorkshire in northern England, since 1972 (Gaston and Lawton 1988, 1989; Heads and Lawton 1984, 1985; Lawton 1976, 1982, 1984a, b; Lawton and Gaston 1989; Lawton and Heads 1984; MacGarvin et al. 1986). The site is described in Lawton (1976, 1982). The insects, together with their essential life-history characteristics, are listed in Table 1. Difficulties in distinguishing different species within the genera *Phytoliriomyza* (Diptera: Agromyzidae–two species) and *Aneugmenus* (Hymenoptera: Tenthredinidae–three species) in field censuses means that these genera are treated as single taxa in the analyses that follow. For simplicity, we often refer to all taxa as "species". Pooling data on two or three species may bias the results in ways that are difficult to foresee. Not all the species known to occur on bracken at Skipwith are included in the present analyses; some occur too infrequently (too many zeros in the census data) for us to carry out tests of density dependence.

Theoretically, the relative and absolute abundances of species in a community may conform to one of four idealized models (Strong et al. 1984; Lawton and MacGarvin 1986; Lawton and Gaston 1989) that result from the underlying population dynamics. These communities represent points on an idealised continuum:

(i) Random assemblages in which density dependence has little effect on any species. Relative abundances are unpredictable and extinctions and colonizations frequent.

(ii) Assemblages in which individual species are independently regulated by factors such as intraspecific competition for resources in an unsaturated community, or natural enemies keep component populations at low levels. Relative abundances are predictable, but interspecific competition is scarce or absent.

(iii) Assemblages in which individual populations are controlled by delayed or over-compensating density dependence. Time delays and/or strong density dependence lead to cyclical fluctuations or deterministically chaotic dynamics. The overall picture is that of an unpredictable community, as in (i). Interspecific competition may occur during periods of peak abundances.

(iv) Assemblages where interspecific competition is important and consistently present. The community has predictable relative abundances and may be saturated with species.

Previous analyses of the bracken assemblage (Lawton and MacGarvin 1986; Lawton and Gaston 1989) suggest that it most closely conforms to a type (ii) community. Thus we might predict that density dependence is present

in the majority of the component populations. We test this prediction here.

Methods

Sampling methods are described in Lawton (1976, 1982). These involve determining mean numbers of individuals per frond on at least 20 randomly selected fronds for each species of herbivore at approximately 2–3 week intervals from May until September. From these data two measures of abundance can be calculated. They are the maximum mean number of individuals per frond for each species each year (peak abundances), and total seasonal abundance of each species, from the area under plots of abundance per frond over the growing season. These two measures are highly correlated (Gaston and Lawton 1989; Lawton and Gaston 1989); accordingly we have restricted analyses in the present paper to peak abundances. There have been no systematic changes in average frond density or in the sizes of the open and woodland bracken patches during the study; hence peak seasonal abundances per frond closely reflect total population sizes of each bracken-feeding insect in the study area.

The data consist of 32 time series of herbivorous insects feeding on bracken at Skipwith Common in North Yorkshire, 17 of 12 years in length collected from the open habitat (1980–1991) and 15 of 8 years duration (1980–1987), collected from the adjacent woodland habitat (Lawton and Gaston 1989). Sampling began at the Skipwith open site in 1972, but prior to 1980 there are some missing years, making the data inappropriate for the present analyses. These earlier censuses do, however, confirm that species' population dynamics (average levels of abundance and amplitude of population fluctuations), have remained broadly similar for nearly 20 years. In accordance with Andrews (1991), failure to record species in any one year (zero abundances) was assumed to represent populations that were too small to measure, rather than an indication of genuine absence. We arbitrarily set zero abundances at 0.1 times the minimum abundance recorded for each species; trial and error suggests that varying the proportion appears to have relatively little influence on rates of detection of density dependence. Table 2 summarizes the number of time series in which Andrews' correction was applied.

Six different tests of density dependence were carried out on each data set, five for direct and one for delayed density dependence. In a seventh test, we examined the data for significant temporal trends.

1. The simplest test was a least-squares regression of k-value ($\ln(N_t/N_{t-1})$) against $\ln(N_{t-1})$ (Varley and Gradwell 1960), where N_t is the abundance at time t. F-tests were used to judge significance at a 5% probability level; the slope was then tested against a slope of zero using a Student's t-test. Errors in the ordinate were assumed to be normally distributed.

2. Bulmer's (1975) first test was carried out using the following formulae:

$$R = V/U$$

$$\text{where} \quad V = \sum_{t=1}^{n} (X_t - \bar{X})^2$$

$$\text{and} \quad U = \sum_{t=1}^{n-1} (X_{t+1} - X_t)^2.$$

X_t is the natural logarithm of abundance at time t. Critical values of R were calculated using $R_{0.05} = 0.25 + (n-2)0.0366$. The null hypothesis of density independence was rejected for values less than or equal to $R_{0.05}$. Note that $\bar{X}$ is the logarithm of the geometric mean of abundance, and *not* the logarithm of the arithmetic mean abundance as stated by Southwood (1978).

3. Bulmer's (1975) second test was investigated, despite criticisms that the test is conservative (Slade 1977; Vickery and Nudds 1984; Reddingius and den Boer 1989). We used the following formulae:

$$R^* = W/V$$

$$\text{where} \quad W = \sum_{t=1}^{n-2} [(X_{t+2} - X_{t+1})(X_t - \bar{X})] \quad \text{and} \quad V = \sum_{t=1}^{n} (X_t - \bar{X})^2$$

Critical values of R^* were calculated using $R^*_{0.05} = (-13.7/n) + (139/n^2) - (613/n^3)$. The null hypothesis of density independence was rejected for R^* values less than or equal to $R^*_{0.05}$. $\bar{X}$ is again the logarithm of geometric mean of abundance.

4. Vickery and Nudds' (1984) test, as modified by Pollard et al. (1987), was carried out using the following sequence of calculations:

a. Regression of $\ln(N_t)$ vs. $\ln(N_{t-1})$ using the observed census data. Student's t was calculated for the difference of the slope from a slope of unity, regardless of the significance of the regression as judged by an F-test.

b. Calculation of the trend in the data set (parameter $\hat{r}$), for which the mean value of d_t, $(\bar{d})$ was used where $d_t = \ln(N_t) - \ln(N_{t-1})$.

c. $$\hat{\sigma}^2 = \sum_{t=1}^{n} \frac{(d_t - \bar{d})^2}{(n-2)}.$$

d. Simulated data sets of the same length as the observed time series were generated using $X_{t+1} = X_t + \varepsilon_t + \hat{r}$, where ε_t values are normally distributed random deviates with zero mean and variance of $\hat{\sigma}^2$, and X_1 comes from the observed time series. Normally distributed random numbers were generated using GLIM's random number generator and normal distribution function (Nelder and Wedderburn 1972). Following Manly (1991) a total of 25000 simulated time series were used.

e. For each simulated time series Student's t was calculated in the same way as step a.

f. The proportion of data sets which had a value of Student's t which was greater than or equal to that of the observed time series was calculated; this proportion is the conditional probability of density independence.

Both this test and the next one (5) compare the time series with density independent time series that can have a temporal trend if such a trend exists in the time series. This is in contrast to regression tests (1) and Bulmer's tests (2, 3), which make no allowances for trends.

5. Pollard et al.'s (1987) permutation test was carried out in the following way:

a. The test statistic, the correlation coefficient between observed population change and the population size itself, was calculated for the observed census data.

b. $X'_1 = X_1$ was calculated, where X'_i $(1 < i < (n-1))$ is used to denote the natural logarithm of abundance in a data set at time i.

c. $d_i = X_{t+1} - X_t$ was calculated. These values were then randomly shuffled using the random number generator in GLIM (Nelder and Wedderburn 1972) to generate uniformly distributed variates which were used as positions in the series, such that the new positions in the sequence were called i for the d_i values. Following Manly (1991) a total of 25000 simulated time series were used.

d. Shuffled data sets were constructed using $X'_{i+1} = X'_i + d_i$ and the test statistic was calculated for each data set.

e. The proportion of values of the test statistic which were larger or equal to the observed value was calculated. This proportion is the conditional probability of density independence.

6. Delayed density dependence is usually looked for with a single method, based on the Ricker (1954) equation, as extended by Turchin (1990),

$$N_t = N_{t-1}\exp(r_0 + \alpha_1 N_{t-1} + \alpha_2 N_{t-2} + \varepsilon_t),$$

where r_0, α_1 and α_2 are model parameters and ε_t is a term to represent sampling error. Density dependence is then detected by regressing $\ln(N_t/N_{t-1})$ against N_{t-1} and N_{t-2} to test the significance of the latter, giving a lag of one and two generations respectively. A lag of 1 generation represents direct density dependence and a lag of 2 generations represents density dependence that is delayed by

Table 2. Comparison of the result of tests of density dependence for bracken-feeding insects on open (O) and woodland (W) sites

Species	Zeros		Trend		Varley and Gradwell's test		Bulmer's first test		Bulmer's second test		Pollard et al.' s test		Vickery and Nudds' test		Delayed density dependence test		Lag in generations	
	O	W	O	W	O	W	O	W	O	W	O	W	O	W	O	W	O	W
B. viridescens	0	2	−	0	−	+	−	+	−	−	−	−	−	−	−	−	−	1
C. albifrons	4		+		−		−		−		−		−		−		−	
C. histricina	0	0	−	0	+	+	−	−	−	−	−	−	−	−	−	−	1	1
C. parvicornis	0	0	0	0	−	−	−	−	−	−	−	−	−	−	+	−	3	−
D. filicina	0	0	0	0	−	−	−	−	−	−	−	−	−	−	+	−	3	−
D. pteridicola	0	0	0	0	−	−	−	−	−	−	−	−	−	−	+	−	3	−
Phytoliriomyza spp.	2	2	0	0	−	−	−	−	+	−	−	−	−	−	+	−	1 & 3	−
D. pteridis	0	0	0	0	−	−	−	−	+	−	−	−	−	−	−	−	1	−
M. ptericolens	2	2	0	0	−	−	−	−	−	−	−	−	−	−	−	−	−	−
M. filicis	0	1	0	0	+	−	−	−	+	−	−	−	−	−	−	−	1	−
Aneugmenus spp.	0	4	0	0	−	+	−	+	+	−	−	−	−	−	+	−	1 & 3	1
S. delicatulus	0	0	0	0	+	−	+	−	−	−	−	−	−	−	+	−	1 & 2	−
S. lineata	0	5	0	0	−	−	−	−	−	−	−	−	−	−	−	−	−	−
T. ferruginea	0	0	+	0	+	−	+	−	−	−	−	−	−	−	−	−	1	−
Tenthredo sp. 2	2	5	0	0	+	+	+	−	−	−	+	−	−	+	−	−	1	1
O. lacunana	5	2	+	0	+	+	+	+	−	−	−	+	−	−	−	−	1	1
P. cytisella	2		0		+		+		−		−		−		−		1	
Total					7	5	5	3	4	0	1	1	0	1	6	0		

Specific names are given in full in Table 1. The column marked zeros gives the number of zero abundances that occurred in the time series. Trend is the sign of the slope of regression of logarithmic abundance against time, a "0" is used to indicate that there was no significant slope. For each test: "+" = density independence was rejected at the 5% probability level. "−" = density independence was not rejected. Blanks indicate that the species did not occur at that site. The row marked total gives the total number of species for which density independence was rejected for each site

1 generation. Here this approach was extended by additionally regressing $\ln(N_t/N_{t-1})$ against N_{t-3} giving a lag of 3 generations, which is equivalent to a delay of 2 generations.

7. Finally, to allow the effects of temporal trends in abundances to be assessed, the presence of a trend was determined for each of the 32 time series by regressing the natural logarithm of abundance against time. The significance of the regression was judged using an *F*-test.

Results

Results are summarized in Table 2. Despite the short duration of the runs of census data, direct density dependence was detected by one or more of the methods in 10 out of 17 taxa (58.8%) in the open site and 5 out of 15 taxa (33.3%) in the woodland site. For the 15 species which occurred at both sites density dependence was detected in at least one site, by at least one method in 10 species (66.7%). Delayed density dependence was detected for a further 3 taxa in the open site, and for 3 taxa where direct density dependence was also found. Hence some form of density dependence was detected in 13 of 17 (76.5%) taxa in the open site and 13 of 15 (86.7%) for taxa which occurred at both sites. Assuming a 5% level of spurious detection we expect eight cases of false detection of direct density dependence (compared with 33 actual cases) and 1.6 cases of spurious detection of delayed density dependence (compared with 6 actual cases). We conclude that density dependence occurs in these time series appreciably more often than expected by chance.

Density dependence was detected more frequently for the open site than the woodland site for all tests, in accordance with the expectation that statistical power increases with increased duration of studies (Solow and Steele 1990; Woiwod and Hanski 1992).

If cases where the census data show a significant trend in logarithmic abundances over time are excluded, these findings are not greatly changed, although sample sizes are reduced (Table 2). No significant temporal trends occurred at the woodland site, even though plots of logarithmic abundance were often similar in appearance for the woodland and open sites. This difference is presumably due to the shorter duration of the woodland time-series. The problem of limited sample size might be expected to become worse in analyses of delayed density dependence. Regressions with 6 points (lag = 2 years) or 5 points (lag = 3 years) for the woodland site all failed to detect delayed density dependence. Equivalent figures were 10 and 9 points respectively for the open site; here, delayed density dependence was found in a total of 6 (35.3%) of the 17 time series.

Regression of *k*-value against logarithmic abundance detected density dependence most frequently; for 7 of 17 species (41.2%) in the open site and in 5 of 15 cases (33.3%) for the woodland site. Pollard et al.'s (1987) test and Vickery and Nudds' (1984) test detected density dependence infrequently (twice and once from 32 cases respectively).

Varley and Gradwell's test identified density dependence in 12 of 32 time-series. In these 12 time-series density dependence was identified by methods other than Varley and Gradwell's test for ten time-series (a total of 12 test results). By contrast, in the 19 time series where Varley and Gradwell's test failed to find density dependence other methods identified density dependence in only 3 time-series (a total of 3 test results).

In the open site there are eight taxa where parasitoids are thought to be consistently present in the life-cycle, and density dependence was found in five (55.5%) of these time-series. Density dependence was found in six (66.7%) of the nine taxa where parasitoids are not thought to be important. The occurrence of delayed density dependence also showed no clear patterns; delayed density dependence, but not direct density dependence occurred in two taxa (25%) where parasitoids are important and one species (11%) where parasitoids are of less importance. Both direct and delayed density dependence occurred for one taxon (13%) where parasitoids are apparent and two taxa (22%) where they are not.

There are eight taxa at the open site which are univoltine and there is no delayed diapause; for these, density dependence was detected by at least one technique in seven taxa (87.5%), compared to only three (33.3%) of the nine taxa with other forms of life-history. Equivalent figures for delayed density dependence at the open site are one (14.3%) and five (55.5%) taxa respectively. This pattern holds when individual tests are considered separately. There are four taxa which were univoltine, that do not have delayed diapauses and where parasitoids are not apparent in the life-cycle. Direct density dependence was detected for all of these taxa and delayed density dependence was found in one of them. In the remaining taxa, density dependence was found in seven taxa (53.8%) and delayed density dependence was found in five taxa (38.5%).

Discussion

The time series analysed consisted of only small numbers of generations (8 and 12). Previous workers have found that the frequency of detection of direct density dependence from time-series of comparable length is low, rarely exceeding 50% for the best available techniques (Vickery and Nudds 1984, 1991; Gaston and Lawton 1987; Hassell et al. 1989). With unusually long time-series Woiwod and Hanski (1992) detected delayed density dependence in less than 5% of time series from aphids and moths, but found direct density dependence in up to 88 and 91% of cases respectively. Turchin (1990) found delayed density dependence in 8 of 14 species of forest insect.

Although we never detected density dependence more often than 41.2% of the time (Varley and Gradwell's test) and as little a 3.1% with Vickery and Nudds' test, overall we detected density dependence considerably more often than would be expected by chance. The detection of density dependence was nevertheless curiously idiosyncratic across methods and for this reason we must be particularly cautious in interpretation. Direct density dependence was found by at least one method in 10 of 17 taxa (58.8%) in the open site and in 5 of 15 taxa (33%) in the woodland site. Delayed density dependence was found for a further 3 taxa in the open site and for 3 taxa in which direct density dependence was also detected. Hence some form of density dependence was found in 13 of 17 taxa (76.5%) in the open site and in 13 of 15 taxa (86.7%) which occurred at both sites.

We found density dependence in 11 of 17 taxa in the open site (12 generations), compared with 5 of 15 taxa at the woodland site (8 generations). That density dependence was found more frequently in longer time series accords with expectations of statistical power (Solow and Steele 1990) and the findings of analyses of time series (Hassell et al. 1989; Hanski 1990; Woiwod and Hanski 1992).

It is not clear why the methods yield such different results, although they are known to differ in power (Solow 1990; Solow and Steele 1990) and bias. The problem of bias has been investigated in terms of spurious detection from density independent simulated data; for Bulmer's (1975) first test departures from the density independent model used by the tests' authors lead to increased rates of spurious detection of density dependence (Solow 1990; Reddingius 1990) and the variance of the time series influenced rates of spurious detection (Reddingius 1990). It is not unreasonable to expect that the degree of similarity between the form of density dependence being tested for and that observed influences the frequency of detection of density dependence. The tests differ in their method of testing. Varley & Gradwell's test has not been formulated in a formal way; values of slope different from zero are thought to represent density dependence. By contrast, critical values of the test statistic in Bulmer's tests have been derived from density independent random-walk data and a given form of density dependent data. Critical values of the test statistic in Pollard et al's test are derived from randomizations of the time series being tested. These differences make regression tests the most likely to spuriously detect density dependence, Bulmer's tests are intermediate in levels of spurious detection and randomization tests are least likely to spuriously detect density dependence. The use of Varley & Gradwell's test could be questioned because the assumption that the two axes are independent is violated. Furthermore, Varley & Gradwell's test is widely reported to be biased (Vickery 1991 and references therein). It is far from clear how conservative tests for density dependence should be. Other reasons for differences in detection rates between the various tests require more investigation.

There are apparently some more biological reasons why we sometimes fail to detect density dependence. The tests for density dependence assume that the population is sampled once each generation, and perhaps not surprisingly density dependence was detected most frequently (87.5% cf. 33.3%) in those species with a single annual generation and which lacked delayed emergence. Delayed density dependence was detected most frequently in taxa with more complex life histories (55.5% cf. 14.3%).

The frequency of detection of both direct and delayed density dependence was apparently not influenced by whether parasitoids were apparent in the life-cycle or not, but the data used to assess the importance of parasitoids are crude, and far from definitive.

From the frequency of density dependence we conclude that the bracken assemblage is most like a type (ii) community (Strong et al. 1984), but the density dependence is not predictably detectable, so that without further information this conclusion must remain tentative.

We conclude that analyses of short time-series are useful and suggest that as well as statistical reasons there are probably biological reasons which explain where we detect density dependence. To be more certain of detecting density dependence and to understand the nature of these processes it will be necessary to turn to intra-generational studies and manipulative experiments.

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