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INJURIES ON STICKLEBACK FROM ATTACKS BY A TOOTHED PREDATOR (ONCORHYNCHUS) AND IMPLICATIONS FOR THE EVOLUTION OF LATERAL PLATES

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Morphological variability in threespine stickleback (*Gasterosteus aculeatus*) has stimulated diverse studies in population differentiation (Hagen and Gilbertson, 1972; Moodie and Reimchen, 1976; Gross, 1978; Giles and Huntingford, 1984), selective predation (Bell and Haglund, 1978; Hagen and Gilbertson, 1973; Banbura et al., 1989), and evolutionary rates in fossil assemblages (Bell and Haglund, 1982). A major theme in this literature is predation and this is associated with differences in robustness of spines and number of bony lateral plates on the trunk. Freshwater populations of stickleback exposed primarily to avian piscivores have two to five plates (Reimchen, 1992) while those exposed to predatory fish usually have more than five plates (Hagen and Gilbertson, 1972; Moodie and Reimchen, 1976; Gross, 1978). Marine populations, which probably encounter a far greater diversity of predators than freshwater populations (Gross, 1978; Reimchen, 1992), have a full complement of 30 to 35 plates. Currently, the only known function of lateral plates is to buttress the dorsal and pelvic spines during predator manipulation (Reimchen, 1983). However, this function is restricted to the 4 plates in the central trunk region and does not account for expression or variation in 3 additional anterior plates or 25 plates posterior to the central trunk.

An obvious advantage of lateral plates other than buttressing the spines could be protection of the trunk from injuries received during attacks by predators. Up to 90% of the attacks on stickleback by predatory fish are failures (Reimchen, 1991*a*), largely due to the presence of dorsal and pelvic spines (Hoogland et al., 1957). Compared with capture by avian piscivores, which produce superficial scars on the fish (Reimchen, 1988), toothed predators would be able to puncture the integument potentially leading to osmoregulatory failure. Remarkably, despite a half a century of study on stickleback (for reviews, Wootton, 1976, 1984; Bell, 1984), the condition and fate of individuals that have escaped from predatory fish is unknown. Such information might provide insight into optimal defenses. In this note, I describe injuries and survival rate of threespine stickleback from attacks by cutthroat trout (*Oncorhynchus clarki*), one of the common toothed predators of this species. Extending from the results, a general hypothesis is proposed for the macrogeographical variation in lateral plates in *Gasterosteus.*

Methods

The work was carried out at Drizzle Lake, Queen Charlotte Islands on the west coast of Canada. This site is the focus of a long-term study designed to partition the relative contributions of different predators to spine and lateral plate evolution in stickleback (Reimchen, 1983, 1988, 1992). Cutthroat trout is 1 of 22 predator species taking stickleback in the lake but it is the single most important species, accounting for about 50% of the total fish consumed (Reimchen, 1990, 1992). Experimental design for the present study is described in Reimchen (1991*a*). Stickleback were collected from the lake and held in littoral enclosures that had a free flow of lake water. All individuals showing evidence of predator-induced injuries were excluded from the experiment. Over an eight-week period (June

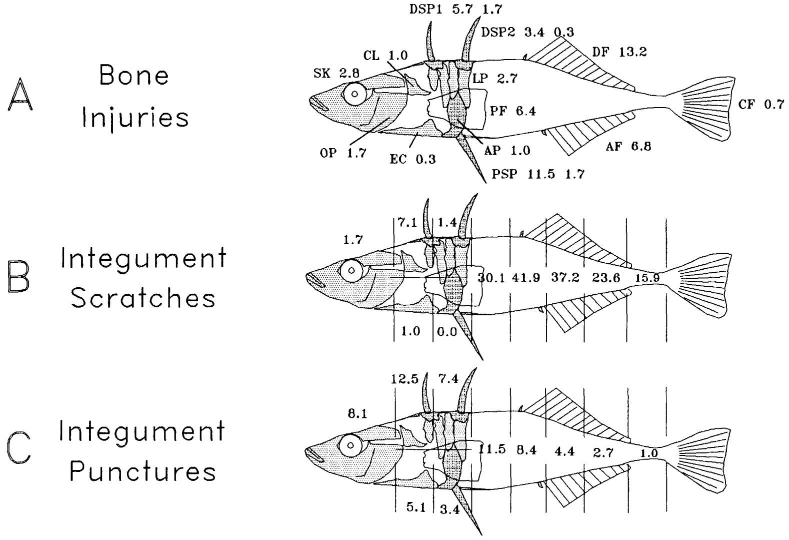

FIG. 1. Incidence of injuries observed on threespine stickleback that have escaped from cutthroat trout. Values show percentage of all fish with injury at each position. A: structural injuries ($N = 296$ fish). Data pairs on spines show 1) minor injuries and 2) major fractures. AF—anal fin; AP—ascending process of the pelvic girdle; CF—caudal fin; DF—dorsal fin; DSP1—dorsal spine 1; DSP2—dorsal spine 2; CL—cleithrum; EC—ectocoracoid; PSP—left and right pelvic spines; LP—left and right lateral plates; OP—operculum; PF—pectoral fin; SK—skull. Stippled regions show distribution of surface bone. B: integumentary scratches ($N = 206$ fish). Percentages for scratches excludes fish with more serious injuries (i.e., punctures) to provide independence. C: integumentary punctures ($N = 296$ fish).

10 to August 10), 1,705 stickleback were added singly to enclosures containing six cutthroat trout. During the first part of the experiment, 153 stickleback that had escaped during manipulation (includes "escapes" and "rejections"—see Reimchen, 1991*a*) were immediately preserved for analyses of injuries. In the latter part of the experiment, 143 individuals that had escaped were maintained in two-liter aquaria (two to six fish per aquarium) and monitored for survival. I recorded the condition of fish at 1 hr and 3 hr after the attack and thereafter at approximately 12-hr intervals. Initially, I monitored fish for up to 12 days but because there was little mortality 2 to 3 days after the trout attack, I shortened the post-attack observation period (minimum 6 days). For statistical purposes, I will use six days as a truncation period and will assume that survival for this period reflects the potential for longer-term survival in nature. As a control, I kept 75 fish in a 20-liter enclosure adjacent to the aquaria for a 10-day period after which they were released and replaced with new fish from the lake for an equivalent period. There was no mortality in the control groups.

On all fish, I recorded under a dissecting scope (10–40×) the type of injury (fractures of surface bone, scratches and punctures of the integument unprotected by surface bone—see Reimchen, 1988). Most of the surface bone of stickleback has complex microsculpturing and I could not reliably identify tooth-induced scratches on this surface. Injuries on both sides of the fish were placed into 1 or more of 10 regions including the head (HEAD), dorsal and ventral cleithrum (DCLT, VCLT), dorsal and ventral buttressing plates (DPLT, VPLT), and five trunk segments between the second dorsal spine and the caudal peduncle (MIDA, MIDB, POSA, POSB, POSC). I distinguished dorsal and ventral halves in the anterior trunk region as there is differential bone cover. Relative area of surface bone and exposed integument were estimated on a planar projection. Spine injuries were separated into three classes (bent, fracture at the tip, major fracture) and fins were scored for damage (ripped membranes). Fish were measured for standard length (SL) and scored for number and position of lateral plates on each side of the body. Due to a nondirectional bilateral asymmetry in number of plates ($r = 0.63$), data on plates were analyzed for the left side of the body (LLP) and for minimum number of plates on either side (PLATEMIN). Statistical results were concordant in all cases but PLATEMIN provided a more conservative description of the data and is therefore used here. The majority of fish in the lake population have from three to five plates per side ($x = 4.8$). Survival time (hr) was log transformed.

RESULTS

Of the 296 stickleback that escaped during trout manipulation, 20.3% had no external injury while those remaining had bone fractures and damage to the integument. Spine damage occurred in 17% of the fish and four-fifths of these involved minor injuries such as small breaks or bends to the tip of the spine. Only 3% of all fish had major spine fractures. The first dorsal spine had the highest and the second dorsal spine the lowest incidence of injury but these differences were not statistically different ($\chi^2_3 = 3.2$, $P = 0.35$). Despite their robust appearance, there was differential struc-

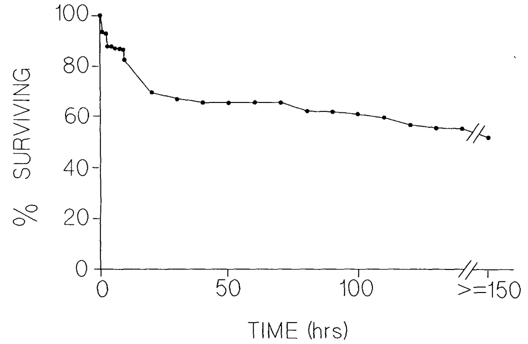

FIG. 2. Survival rate of threespine stickleback following attack by cutthroat trout. Total sample size at beginning of experiment equals 143 individuals.

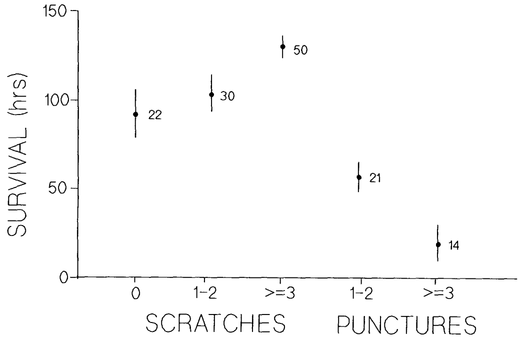

FIG. 3. Survival time (±1 SE) and level of injury for threespine stickleback following attack by cutthroat trout. Sample sizes shown adjacent to means.

tural integrity of bony plates with 9% of the fish having fractures. These included the ectocoracoid, the ascending process of the pelvic girdle, the lateral plates buttressing the spines, and the cleithrum (Fig. 1A). As well, the roof of the skull was crushed, commonly at the suture between the dermosupraoccipital and frontal bones. Among fish with fractured plates, underlying tissues were often damaged, occasionally extruding through the fracture on to the plate surface.

Fin membranes were torn (usually fewer than four rays were affected) in 21% of the fish (Fig. 1A). The dorsal fin sustained the greatest and the caudal fin the least number of injuries ($\chi^2_3 = 36.8$, $P < 0.001$). The pectoral fin also had few injuries, but when present, these involved damage at the insertion of the rays and would presumably affect fin function.

Integumentary injuries occurred on 70% of all fish (scratched—55.4%; punctured—31.4%). Integument is exposed on all of the posterior half of the stickleback and on 34% of the anterior half. Frequencies of integumentary injuries should be much lower in anterior positions because of the reduced proportion of exposed integument. For scratches, this is confirmed, these being an order of magnitude less abundant on the anterior than the posterior half of the fish ($\bar{x} = 0.13$ versus 1.66, paired $t\text{-test}_{295} = 14.3$, $P < 0.001$, Fig. 1B). However, the distribution of punctures shows no such trend, for these were equally abundant in anterior and posterior halves ($\bar{x} = 0.40$ versus 0.36, paired $t\text{-test}_{295} = 0.60$, $P = 0.55$, Fig. 1c). The number of fish injured for each group shows a comparable trend to total number of injuries. There was an excess of fish with scratches on posterior regions (anterior—11.8%, posterior—54.7%) but a similar number of fish with anterior and posterior punctures (anterior—21.3%, posterior—17.6%). Punctures rarely occurred on the armor, but rather, were found on exposed integument between the bony plates. These were most prevalent immediately behind the head and were more frequent in dorsal than in ventral segments (Wilcoxon signed-rank test, DCLT versus VCLT, $Z = 3.5$, $P < 0.001$; DPLT versus VPLT, $Z = 2.6$, $P < 0.01$). Although lacking surface armor, VCLT has a broad bony plate (scapula and coracoid) that immediately underlies the integument and this will limit tooth penetration.

Among 143 stickleback monitored for postattack survival, mortality was high within the first 24 hours, during which 33% of all fish died. Thereafter, survival remained high (Fig. 2). At the completion of the experiment, 51% of the fish were alive and none exhibited obvious symptoms of trauma. Unmarked and scratched fish had high survival relative to those with punctures. Of 80 fish with scratches, 58 were alive after six days but of 35 fish with punctures, 5 survived ($\chi^2_1 = 11.8$, $P < 0.001$). Similar trends are reflected in average survival time as fish with the greatest number of punctures had the lowest survival (ANOVA $F_{4,132} = 14.2$, $P < 0.001$, Fig. 3). An exception to this association occurred among unmarked and scratched fish, for in these, survival was significantly higher among fish with multiple (> = 3) than with few or no scratches (Student-Neuman-Keuls procedure, $P < 0.01$). This anomaly may simply be an artifact of scoring. Fish become progressively pale with prolonged captivity and integumentary scratches are more visible on these fish than on melanistic individuals. This would lead to higher scratch scores for the longest survivors.

I analyzed whether position of injury on the body surface influenced relative survival. Among the 10 body sections, those in the postcranial and dorsal spine region (DCLT, DPLT, MIDA) yielded the highest negative correlations with survival ($r > 0.25$, $P < 0.001$) although these also gave highly significant pair-wise correlations among body positions (Table 1). Multiple regression ($r = 0.48$, $P < 0.001$) and statistical removal of correlated responses identified three significant predictors of survival—DPLT (partial $r = -0.29$, $P < 0.001$), DCLT (partial $r = -0.27$, $P < 0.001$), and HEAD (partial $r = -0.19$, $P < 0.001$) demonstrating that anterior body positions contributed more to variance in survival than posterior regions.

Individuals varied in the number of lateral plates on the anterior trunk (positions 3–8), providing an opportunity to evaluate differential plate expression and injury in the postcranial region. If the plates function as armor, one predicts reduced injury and increased survival on fish with increased number of plates. The data are consistent with this prediction (Fig. 4).

I calculated a single index of injury based on the cumulative number of punctures from all segments and incidence of major fractures to spines and tested for correlations with survival, number of lateral plates (PLATEMIN) and SL. These data show significant correlations among variables including LOGSURV ×

PLATEMIN and LOGSURV × SL (Table 2). Multiple regression analysis ($r = 0.50$), undertaken to partition these interactions, gave two significant predictors of *survival*: INJ (partial $r = -0.45$, $P < 0.001$) and PLATEMIN (partial $r = 0.20$, $P < 0.02$). SL did not contribute a unique effect to LOGSURV (partial $r = 0.13$, $P = 0.14$).

DISCUSSION

Prey with low palatability are generally resistant to injury (Vermeij, 1982 for review). Manipulation time of threespine stickleback attacked by cutthroat trout averaged 52 s and during this period, the stickleback are subject to extensive biting and rotation in the mouth of the trout (Reimchen, 1991*b*). Data presented above show that the stickleback escaping during this manipulation vary substantially in their level of injury, from unmarked through to massive puncturing of the integument and fractures of bony plates. Survival was inversely proportional to the level of intrusive injuries. This variability in postattack survival provides opportunity for selection to operate on structures that influence likelihood of intrusive injury.

Substantially more integumentary punctures occurred on the anterior trunk than expected given the relatively small surface area of exposed integument in this region. This suggests increased jaw contact compared with posterior regions of the body and ensues from the tendency for predatory fish to direct the initial strike towards the head (Hoyle and Keast, 1987, 1988) or towards the center of mass of the prey (Webb, 1984). Even when attacked tailfirst, prey are rotated into a headfirst alignment for manipulation prior to swallowing (Reimchen, 1991*b*), and this will also increase jaw contact with the anterior body. The evolutionary consequence of this directionality of attack probably contributes to the robustness of head and anterior armor observed in *Gasterosteus.*

Major geographical variation in number of lateral plates occurs in threespine stickleback, ranging from populations without plates to those with a full complement of 30 to 35 plates. Populations without predatory fish tend to have few plates, usually the two to five structural plates that buttress the dorsal and pelvic spines. Avian piscivores probably occur in the majority of these populations and the buttressing plates may be sufficient against attacks by these predators (Reimchen, 1988, 1992). One of the associations observed in western North America and western Europe is that stickleback populations exposed to predatory fish tend to have five to eight plates (Hagen and Gilbertson, 1972; Moodie and Reimchen, 1976; Gross, 1978); this involves the buttressing plates in addition to three anterior plates above the cleithrum (Reimchen, 1983). Data presented here demonstrate that the incidence of punctures near the cleithrum accounts for substantial variance in survival time. This, combined with increased survival of individuals with more plates in this region, can explain the prevalence of these plates in populations were toothed predators predominate.

Given the protective advantages of plates during manipulation by toothed predators, it is remarkable that during the repeated colonizations of freshwater by fully plated marine stickleback (cf. Hagen and McPhail, 1970), there has been recurrent loss of posterior plates. Reduced numbers of predator species probably occur in freshwater habitats (Gross, 1978), yet there are no

TABLE 1. Correlation matrix for incidence of puncturing among body positions and survival. $N = 143$ fish.

	HEAD	DCLT	VCLT	DPLT	VPLT	MIDA	MIDB	POSA	POSB	POSC	LOGSUR
HEAD	1.0	0.33**	0.20	−0.01	−0.05	−0.08	0.09	−0.05	−0.04	−0.02	−0.25
DCLT		1.0	0.47**	0.30**	0.18	0.17	0.06	0.06	−0.05	0.25*	−0.37
VCLT			1.0	0.09	0.03	0.10	−0.05	−0.05	−0.04	−0.02	−0.24
DPLT				1.0	0.79**	0.61**	0.06	0.34**	0.17	−0.03	−0.35
VPLT					1.0	0.40**	−0.04	0.17	0.24*	−0.16	−0.19
MIDA						1.0	0.10	0.25*	0.15	−0.02	−0.26
MIDB							1.0	0.38**	−0.03	0.44**	−0.20
POSA								1.0	−0.24*	−0.02	−0.17
POSB									1.0	−0.01	−0.12
POSC										1.0	−0.15
LOGSURV											1.0

* $P < 0.01$; ** $P < 0.001$.

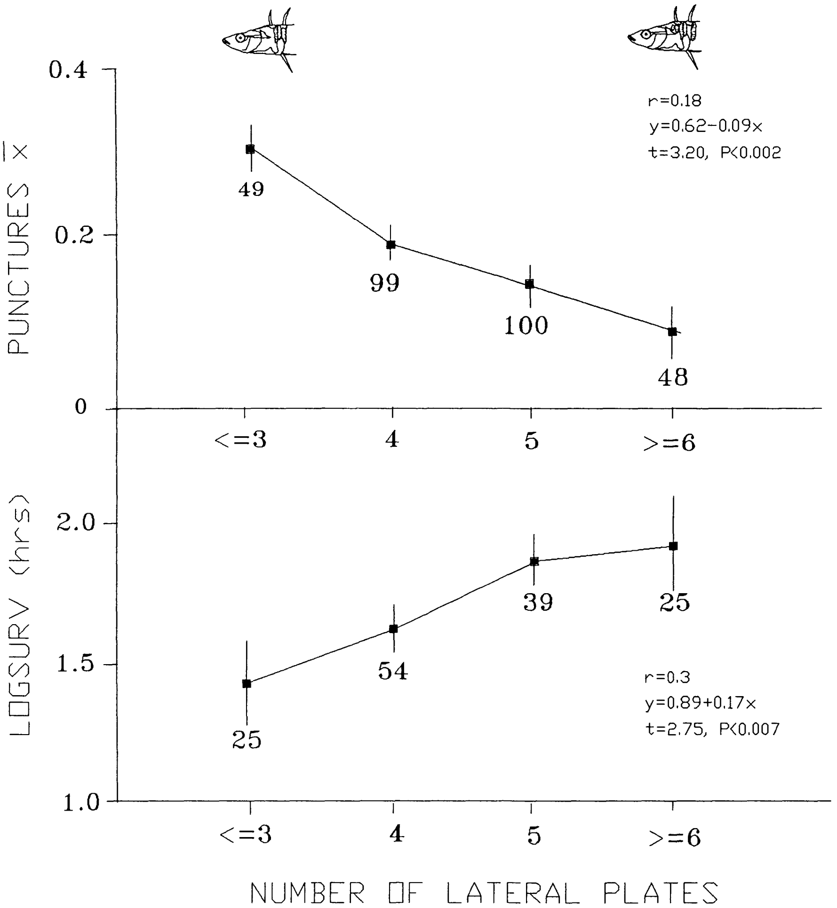

FIG. 4. Upper figure: mean number of punctures (±1 SE) in postcranial region against number of lateral plates ($N = 296$ fish). Bottom figure: mean survival time (±1 SE) against number of lateral plates ($N = 143$ fish). Insets show schematic of anterior trunk of stickleback with three and six lateral plates.

current empirical data to support a suggestion of reduced predator selection in freshwater relative to marine habitats. Intensive life-history analyses of several lake populations demonstrate extensive mortality of stickleback from resident predators (Moodie, 1972; Hagen and Gilbertson, 1973; Reimchen, 1992). Hagen and Moodie (1982) observed a geographical correlation between plate number and climate and propose that low plated stickleback are favored where climate is warm, while fully plated individuals have a selective advantage where winters are cold and yearly temperature range is great. How this selection might operate is unknown.

Hydrodynamic factors provide a possible mechanism for the loss of posterior bony plates in stickleback. Bony armor constrains swimming ability (Aleyev, 1977) and it is generally assumed that the multiple occurrences of armor reduction during the evolution of fishes were associated with a shift to more active swimming roles (Carroll, 1988). If so, reduced number of plates in stickleback might produce increased escape acceleration. The only evidence to bear on this comes from Taylor and McPhail (1986) who found that freshwater stickleback (low-plated morph) exhibit better burst swimming performance relative to marine stickleback (fully plated morph). Because aquatic predator pursuits tend to be only several seconds in duration (Weihs and Webb, 1983), burst velocity for the prey is a critical factor during the pursuit phase. This is temperature-dependent in fishes (Weihs and Webb, 1983) and as such, climatic differences among regions are expected to influence pursuit and manipulation events.

Combining observations on injuries, postcapture

TABLE 2. Correlation matrix for total punctures (all positions), lateral plates (minimum number), standard length of fish and survival of 143 stickleback that escaped during manipulation from cutthroat trout.

	INJ	PLATE-MIN	SL	LOGSURV
INJ	1.00	−0.14	−0.16	−0.46**
PLATEMIN		1.00	0.27**	0.25*
SL			1.00	0.23*
LOGSURV				1.00

* $P < 0.01$; ** $P < 0.001$.

survival and hydrodynamics, it is possible to formulate a general hypothesis on geographical variation in lateral plates. If there are population differences in the relative contributions of predator pursuit and manipulation failures in the life history of the stickleback, differing selective pressures should occur. Number of lateral plates is predicted to be low where probabilities of pursuit escapes are high. This could occur either in habitats where shelter is available or where swimming speeds of prey and predator are closely matched (for example, with small-bodied predators). As the probability of capture rises, selection should favor increased expression of lateral plates, in particular, where toothed predators predominate. This could occur in open water conditions where shelter is less available or where relative swimming speeds are overwhelmingly in favor of the predator (and thus, where capture is likely). Within each habitat defined by the relative contribution of pursuit and manipulation escapes, expression of plates could be influenced by at least two supplemental factors: 1) ratio of toothed and nontoothed predators for all manipulation failures and 2) differences among predators in approach and strike positions (Reimchen, 1991*b*). Studies are underway to test aspects of this hypothesis for micro- and macrogeographical differences in lateral plate distribution.

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RELATIVE RESISTANCE OF GOLDENROD TO APHID ATTACK: CHANGES THROUGH THE GROWING SEASON

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Genetic variation for resistance to insect attack has been documented in many natural plant populations (Berenbaum et al., 1986; Fritz et al., 1987; Karban, 1987; Maddox and Root, 1987; Rausher and Simms, 1989), and herbivory is generally thought to be detrimental to plant fitness (Mattson and Addy, 1975; Morrow and LaMarche, 1978; Janzen, 1979; Rausher and Feeny, 1980; Marquis, 1984; Sacchi et al., 1988; but see Paige and Whitham, 1987; Maschinski and Whitham, 1989). These two observations suggest that insects may impose natural selection on their host plants (e.g., Rausher and Simms, 1989). Plants that are more resistant suffer less herbivory and have higher fitness, and these fitness differences lead to the evolution of resistance in plant populations. Nonetheless, the importance of natural selection imposed by insects on plants as a determinant of extant plant-insect associations is currently being debated (Bernays and Graham, 1988; Rausher, 1988). Some authors argue that insects are usually rare in space and time, and therefore herbivory is rarely an important determinant of plant fitness (Jermy, 1984). Others argue that even if insects are usually rare, when they do become common herbivory can be so devastating to plant fitness that they impose strong selection for resistance to herbivory in their hosts.

These points of view might be reconciled by closer examination of plant resistance to herbivory and the effect of herbivory on plant fitness. For example, relative resistance to herbivory might change through the growing season. If so, which plant genotypes suffer the most herbivory will vary through the growing season, and net fitness differences, measured as seed set or cumulative growth at the end of the season, might be small. Moreover, conclusions about selection imposed by insects might depend on when resistance was measured. Suppose that the plant genotypes most resistant to herbivory early in the season tend to be less resistant late in the season, but that averaged over the whole season plants most resistant early are most resistant overall. Also suppose that herbivory is detrimental to plant fitness. If herbivory were measured early in the season a selection analysis would indicate that insects impose selection on their host plant. On the other hand, if herbivory were measured late in the season such an analysis would suggest that insects do not impose selection on their host plant. Alternatively, herbivory late in the season might be more detrimental to plant fitness than herbivory early in the season. If so, a selection analysis that employed either total or only early herbivory would erroneously conclude that insects do not impose selection on their host plant.

Most studies examining the effect of herbivory on plant fitness have treated resistance to herbivory as a static attribute of plants and have only measured resistance during a small segment of the growing season. However, at least two processes could result in changes in relative resistance through the growing season. First, plant quality as insect food often changes through the growing season as new leaves mature and toughen (Feeny, 1970; Rausher, 1981) or as secondary chemical composition changes (Feeny, 1970; Cooper-Driver et al., 1977; Mooney et al., 1980; Kraft and Denno, 1982; and see Krischik and Denno, 1983, for review). If these changes occur at different rates in different plant genotypes, then which plant genotypes are most resistant to insect attack may change through the growing season as well. Second, environmental conditions can affect which plant genotypes are most resistant to insect attack (Wood and Starks, 1972; Service and Lenski, 1982; Maddox and Cappuccino, 1986; Hughes and Hughes, 1988). If environmental conditions change through the growing season then which plant genotypes are most resistant to insect attack could change as well.

In this paper I present data demonstrating that relative resistance of the goldenrod *Solidago altissima* to the aphid *Uroleucon tissoti* changes during the growing season. Changes in relative resistance reflect underlying changes in effective aphid colony growth rates on different goldenrod genotypes. Moreover, the changes in relative resistance appear to be caused by goldenrod genotypes responding differently to changing environmental conditions. These data suggest that to understand the selection imposed by herbivorous insects on their host plants it will be necessary determine whether relative plant resistance is stable through time.

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