

COSTS AND BENEFITS OF TERRITORIALITY: BEHAVIORAL AND REPRODUCTIVE RELEASE BY COMPETING APHIDS¹

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Abstract. Colonizing stem mothers of the gall-forming aphid *Pemphigus betae* defend gall sites on narrowleaf cottonwood, *Populus angustifolia*. Kicking-shoving contests are used to establish microterritories 3–5 mm in length. The largest stem mothers usually win in competitive bouts. Small differences in body size (i.e., a 3.4% difference in prothorax widths) are more importantly associated with territorial interactions than with fecundity. Stem mothers that win the superior basal position of a leaf produce an average of 56% more progeny than stem mothers displaced to inferior distal positions. Differences in reproductive performance within a leaf result from microhabitat variation in leaf quality. A change of only a few millimetres in the position of the gall on the leaf blade affects aphid reproduction.

Experimental removal of either member of a competing pair allows the remaining stem mother to cross the former territorial boundary and enlarge her own territory. The impact of competitive release on reproductive success is asymmetrical. The distal stem mother of a competing pair achieves an average 48.5% increase in number of progeny, whereas the basal stem mother achieves an 18.5% increase in number of progeny.

Because both members of a competing pair suffer reduced success from competitive interactions, selection favors stem mothers that occupy leaves singly. The largest stem mothers are solitary; their despotic behavior prevents smaller competitors from settling.

Key words: aphid; asymmetrical competition; behavior; body size; competition; competitive release; despotism; *Pemphigus betae*; *Populus angustifolia*; reproductive success; territory.

INTRODUCTION

The goal of this paper is to quantify the reproductive benefits and costs of territorial behavior. As Davies (1978a) observes, direct measures of fitness are difficult to obtain; such data are rare for both vertebrates and invertebrates. Three major questions are addressed. First, with the removal of a competitor does behavioral and reproductive release follow? Second, what are the reproductive costs of losing and the benefits of winning? Third, how is "winning" in a territorial dispute affected by asymmetries in body size and what are the impacts on reproduction?

Although territoriality in asocial insects is recognized as widespread in diverse taxa, the majority of studies deal with *mature males* and their competitive interactions for mates (Baker 1983, Fitzpatrick and Wellington 1983, Thornhill and Alcock 1983, but see Hart 1984). Whether or not this represents a true pattern or simply reflects current research biases is unclear. Here I examine the interactions of *immature females* of the gall-forming aphid *Pemphigus betae*, which aggressively defend superior gall sites or feeding territories on the leaves of narrowleaf cottonwood, *Populus angustifolia* (Whitham 1979). No males are present at this stage of the life cycle and female competition is based solely on the defense of feeding sites that vary greatly in quality (Whitham 1978, 1980). Due to the small size of competing 1st-instar aphids (0.6 mm in

length) and the short duration of their territorial behavior (≈ 3 d/yr), it would not be surprising if similar behaviors were overlooked in other systems.

Each female sexual of *P. betae* oviposits a *single* overwintering egg that emerges in the spring as a wingless fundatrix or stem mother (Harper 1963). Emergence is synchronized with bud break of the host tree; over a 3-d period as much as 83% of the stem mothers migrate to the developing leaves where they initiate galls (Whitham 1978). On a mature tree this cohort can be as large as 81 000 stem mothers (Whitham 1983), and densities may be as high as 850 stem mothers/1000 leaves (T. G. Whitham, *personal observation*). By the stem mother's probing of the expanding leaf tissues, a small depression is formed. Within 3 d the stem mother is enveloped within a hollow gall where she parthenogenetically produces up to 300 progeny. Mortality can be high during these 3 d; on some resistant trees none survive (Whitham 1981, 1983, and T. G. Whitham, *personal observation*).

The preferred gall sites are the bases of the largest leaves. These leaves have the lowest concentration of phenolics (Zucker 1982); are natural resource "sinks" (Way and Cammell 1970); are least susceptible to premature leaf fall (Williams and Whitham 1986); and result in the highest production of progeny (Whitham 1978). Although strong selection pressures are exerted upon stem mothers to settle on large leaves, these preferred leaves are relatively rare (Whitham 1978, 1980). Consequently the stage is set for competition and territorial behavior.

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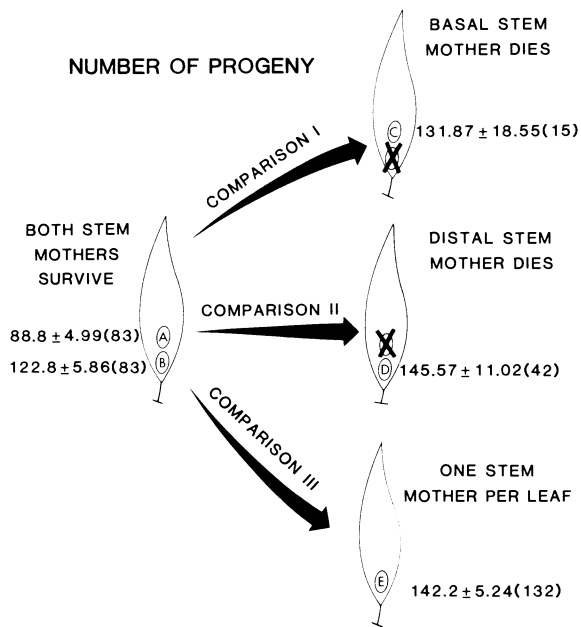


FIG. 1. When either stem mother of a competing pair suffered an early death, the remaining stem mother produced significantly more progeny (Comparison I, $A < C$; Comparison II, $B < D$). Stem mothers occupying leaves singly from the beginning of gall formation produced more progeny than either member of a competing pair (Comparison III, $A < B < E$). When released from competition early in development (i.e., one member of a competing pair died) the surviving stem mothers on average produced the same number of progeny as stem mothers that were solitary from the beginning of gall formation ($C = D = E$). Since leaf size is significantly correlated with the number of progeny, leaves were matched for size to hold leaf quality constant for all comparisons. Mean numbers of progeny ± 1 SE (n) are shown for 355 surviving stem mothers.

METHODS

From 1979 to 1982 studies were conducted on trees along the Weber River near Ogden, Utah. Gall-forming behavior was quantified by measuring the movements of colonizers. Stem mothers move parallel to the midrib of the leaf blade and induce the production of a gall by inserting their stylets into the leaf tissues. Using a dial caliper, the position of each stem mother on the leaf blade (i.e., distance from the stem mother to the leaf base) was measured every 10–15 min during daylight hours.

Removal and addition experiments were performed by using a Number 0000 paint brush to move stem mothers. Their movements and interactions with other stem mothers both before and after manipulation were quantified. Considerable caution was used in moving stem mothers and in handling the host leaf. No apparent effect on aphid behavior was observed.

To examine the potential for competitive release on aphid reproduction, three comparisons were made. The reproductive successes of stem mothers that shared a leaf (A and B in Fig. 1) were compared with the suc-

cesses of stem mothers that occupied leaves singly. Stem mothers occupying leaves singly were divided into three classes: stem mothers in which the basal competitor died of natural causes during the first 3 d of gall development (C in Fig. 1), the opposite comparison in which the distal stem mother suffered an early death (D), and stem mothers that were solitary from the onset of gall formation (E).

Reproductive success was measured by counting the number of progeny produced per stem mother prior to gall maturation in late June and early July, $\approx 2\frac{1}{2}$ mo after gall initiation in mid-April. In July the gall dehisces and the mature progeny migrate to a secondary host. Galls were collected over a 2-d period, frozen, and later examined. Because colonizing stem mothers initiate their galls during a 3-d period at bud break, the aphid population can be treated as a cohort.

To examine the importance of body size in competitive interactions, 1st-instar stem mothers that had just settled were collected. Solitary stem mothers and those sharing leaves were collected in a single day. All leaves were at the same stage of development and aphid territories were actively being established and defended. Prothorax widths were measured at $400\times$ using a compound microscope, and the measurer did not know which aphid categories were being selected.

RESULTS

Effects of density on reproductive success

Solitary stem mothers produced more progeny than stem mothers that shared leaves. Fig. 1 shows the progeny production of 355 stem mothers that either occupied leaves singly, shared a leaf with another stem mother, or inherited a leaf owing to the early death of another stem mother. Because leaf size is significantly correlated with reproductive success (Whitham 1978), the mature leaves were matched for size in all comparisons. The mean leaf sizes ± 1 SE were 13.9 ± 0.30 , 14.4 ± 0.76 , 13.9 ± 0.46 and 13.9 ± 0.24 cm^2 for leaves occupied by galls A and B, C, D, and E, respectively.

Comparisons I and II show that competitive interactions acted in both directions; each stem mother negatively affected the reproductive success of the other. When the basal stem mother of a competing pair suffered an early death, the distal stem mother realized increased reproductive success (Comparison I). Analysis of variance (followed by Student-Newman-Keuls, SNK) shows the success of stem mother $A < B$ ($P < .01$) and the number of progeny of stem mother $B = C$ ($P > .05$). Comparison II shows the reverse situation; when the distal stem mother died, the reproductive success of the basal stem mother increased (AN-OVA-SNK, $A < B$, $P < .01$; $B < D$, $P < .05$).

The effects of removal were not symmetrical. With the loss of the distal competitor the basal stem mother produced an average of 23 more progeny (an 18.5%

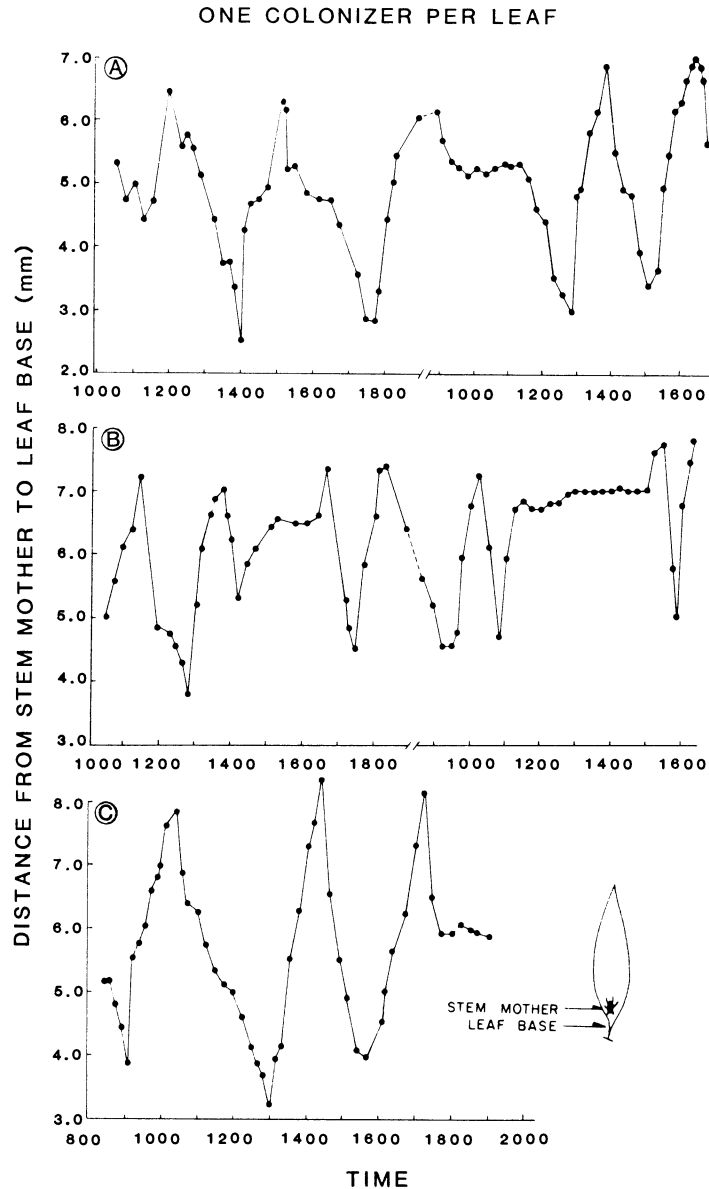


FIG. 2. Shown are the movement patterns of three solitary stem mothers during gall formation. The position of each stem mother on the leaf blade was measured every 10–15 min for 1–2 d.

increase), whereas in the reverse situation the distal stem mother produced 43 more progeny (an 48.5% increase). Thus, the distal stem mother of a competing pair realized nearly twice the benefit.

Stem mothers that occupy leaves singly from the onset of gall formation should also produce more progeny than stem mothers that share a leaf (Comparison III). As predicted, ANOVA-SNK shows the success of stem mother A < B ($P < .01$) and both are < E ($P < .01$). Stem mothers that occupied leaves singly (E) realized 15.8% more progeny than their basal counterparts (B) and 60.1% more progeny than the distal stem mothers (A).

If a competitor died within the first 3 d of gall formation, the remaining stem mother suffered no ill effects from the interaction. Stem mothers released from competition by the early death of a competitor (C and D) achieved success equal to stem mothers that occupied leaves singly (E) from the onset of gall formation (ANOVA-SNK, $C = D = E$, $P \gg .05$).

Stem mothers that die during the brief gall-forming period leave a scar on the leaf as evidence of their failed attempt (Whitham 1978). By including these early colonizer deaths that resulted in zero progeny, the expected reproductive success of the colonizing population can be estimated. The average colonizing stem

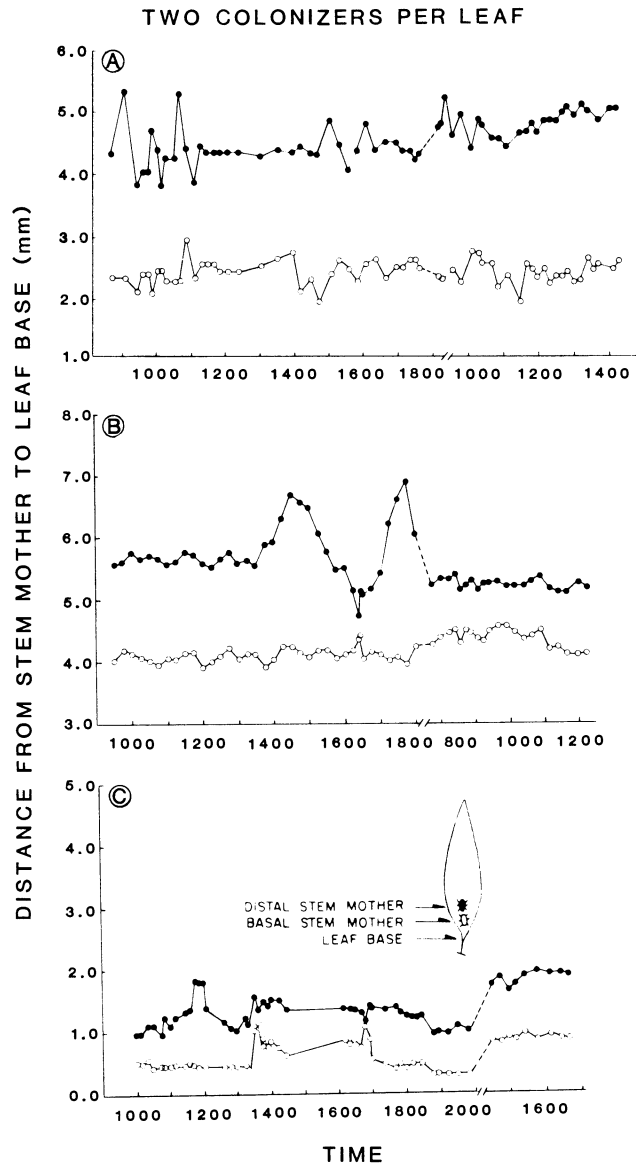


FIG. 3. Shown are the movement patterns of three competing pairs of stem mothers during gall formation. When two stem mothers shared the same leaf their gall-forming behavior was altered; most of their time was engaged in kicking-shoving contests and they rarely crossed a common boundary.

mother occupying a leaf singly can expect to produce 100.7 ± 5.8 progeny ($n = 215$), the basal stem mother of a competing pair can expect 80.8 ± 6.1 progeny ($n = 149$), and the distal stem mother can expect 51.7 ± 4.7 progeny ($n = 172$). In agreement with the results of Fig. 1, these comparisons produced significant differences (ANOVA-SNK, $P < .01$).

Gall-forming behavior of solitary females

The probing behavior of the colonizing stem mother on the immature leaf determines the size and shape of the mature gall. If the stem mother dies within the 1st d of probing, the rudimentary gall enlarges as the leaf tissues expand, but it fails to close. These galls are

much smaller than ones containing a living stem mother (see also Dunn 1960).

The probing of leaf tissues by *P. betae* produces a linear pocket-shaped gall. Fig. 2 shows three replicates of the normal probing movements in which the positions of solitary stem mothers were recorded every 10–15 min over a 1–2 d period. Stem mothers continuously fed and/or probed the leaf tissues with their stylets. Within the 1st d probed tissues began to sink below adjacent nonprobed tissues, and by the 3rd d a pocket was formed that had closed over at the top.

The amplitude of the probing movements is an important behavioral trait correlated with subsequent reproductive success. In Fig. 2, the amplitude of the prob-

ing movements is the difference between the greatest recorded distal and basal positions on the leaf blade. The amplitude is correlated with the length of the mature gall ($r = .459, P < .001, n = 62$), and the length of the mature gall is correlated with the number of progeny found within ($r = .674, P < .001, n = 36$). Only leaves of the same size were compared.

Gall-forming behavior in the presence of a competitor

The negative effects of competition on reproduction were caused in part by a change in the normal gall-

forming behavior. In the absence of a competitor, solitary stem mothers achieved greater amplitudes than competing stem mothers (Figs. 2 and 3). The amplitude of the probing movements of solitary stem mothers averaged 5.38 ± 0.18 mm ($n = 41$ females), whereas competing stem mothers averaged only 3.38 ± 0.20 mm ($n = 39$). This represents a 59% larger amplitude for solitary stem mothers ($t = 7.321, df = 71, P < .001$).

Competing stem mothers also spent less time feeding and/or probing leaf tissues because they spent nearly all their time at the boundary between territories engaged in aggressive interactions. During 48 h of ob-

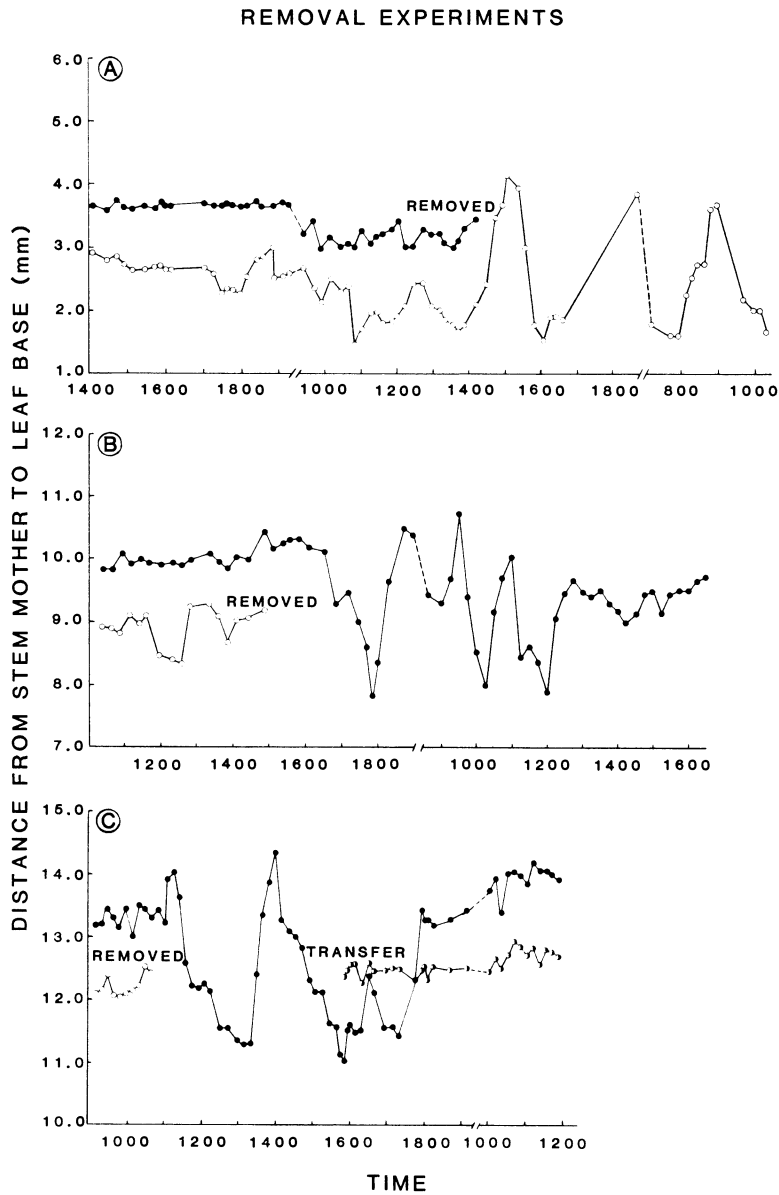


FIG. 4. With the removal of either the distal or basal stem mother (A, B, and C), the remaining stem mother crossed into alien territory and incorporated it into her own. In (C), where the positions of two stem mothers were reversed, after 2 h of kicking-shoving contests they reverted at 1745 to positions previously held, suggesting differences in competitive abilities.

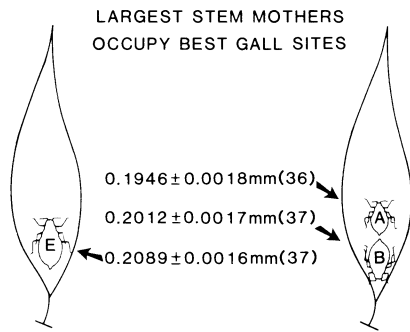


FIG. 5. The largest 1st-instar colonizers settled where the expected production of progeny was greatest. The largest stem mothers were solitary while smaller stem mothers shared a leaf and suffered the negative effects of competition. Solitary stem mothers (E) were larger than the basal stem mothers of competing pairs (B), which in turn were larger than their distal competitors (A). Mean prothorax widths ± 1 SE (n) are shown; all body size categories are significantly different (ANOVA-SNK, $P < .01$).

servation of three competing pairs (Fig. 3), in only 3 out of 175 observations did their positions overlap. Although stem mothers rarely overlapped, they repeatedly engaged in end-to-end kicking-shoving contests during which no feeding or probing occurred. These contests sometimes lasted as long as 2 d, and could result in the death of one or both aphids. Since only rapidly expanding and immature leaf tissues are susceptible to gall formation (≈ 3 d), aggressive interactions came at the expense of gall formation and subsequent reproduction for both competing individuals.

Manipulation experiments of behavioral competitive release

With the removal of a competitor, the remaining stem mother crossed over into alien space, demonstrating that these aphids defend a microterritory (Fig. 4). When the distal stem mother of a competing pair was removed, the basal stem mother crossed the previous boundary and incorporated the territory of her competitor into a new enlarged territory (Fig. 4A). The reverse removal experiment (i.e., the basal stem mother was removed, Fig. 4B) resulted in a similar change in behavior; the distal stem mother crossed into alien territory and incorporated it into her own. In both instances, prior to removal, little feeding and/or probing of leaf tissues was observed, whereas after the removal of competitors, the remaining stem mothers actively fed and/or probed leaf tissues.

Switching experiments suggested that basal stem mothers were competitively superior to distal stem mothers. Fig. 4C shows two experiments; the first involves the removal of the basal stem mother, and the second examines the competitive outcome when positions are reversed. As in previous experiments, when the basal competitor was removed, the remaining stem mother crossed the boundary and established a new,

enlarged territory. At ≈ 1545 a basal stem mother from another competing pair was transferred onto the leaf but placed in the inferior distal position (i.e., positions now reversed). A kicking-shoving contest began that lasted for ≈ 2 h. At 1745 the basal stem mother moved back to the inferior distal position she had occupied at the beginning of the day. Thus, when another competitor was introduced, the resident was displaced. Such displacements were common. As many as 24 stem mothers have been observed trying to colonize the same leaf, but most soon dispersed. The next section examines a likely mechanism for determining the outcomes of disputes.

The importance of body size

If body size is important in determining the outcomes of territorial interactions, then the largest stem mothers should settle where expected fitness is greatest. From the reproductive success data in Fig. 1, superior gall sites can be ranked according to the expected number of progeny; the highest success goes to solitary stem mothers (i.e., E), then to stem mothers that share leaves but occupy the leaf base (B), and last, to those that share leaves but occupy the distal gall position (A).

As predicted, colonizing stem mothers competitively sorted out according to body size; the largest stem mothers were solitary, while smaller stem mothers shared leaves (Fig. 5). The prothorax widths of solitary stem mothers (E) were 3.8% larger (ANOVA-SNK, $P < .01$) than the basal stem mothers (B) of competing pairs, which in turn were 3.4% larger ($P < .01$) than distal stem mothers (A). Since the very largest stem mothers were solitary, it appears their despotic behavior prevented others from settling on the same leaves. These findings are consistent with earlier results showing basal stem mothers were 6.3% larger than their distal competitors ($P < .005$, Whitham 1979).

Micro-habitat differences in leaf quality

Two hypotheses may account for the observed differences in success when two stem mothers share the same leaf. Basal stem mothers can expect to produce 81 progeny (including both survivors and those that die attempting to form a gall) while distal stem mothers can expect to produce only 52. Either the larger basal stem mothers are more fecund and/or the basal position on the leaf is innately superior.

The body-size hypothesis is eliminated by the findings of the competitive release experiments. When released from competition the smaller distal stem mothers produced the same number of progeny as the large solitary stem mothers that had never shared a leaf (see Fig. 1, $C = E$). Similarly, when the smaller basal stem mothers were released from competition they also realized increased success equal to solitary stem mothers ($D = E$, ANOVA-SNK, $P \gg .05$ in both cases).

The basal position of the leaf blade is innately superior to more distal gall sites. Ideally, position effects

could best be examined by holding gall density and leaf quality constant and allowing only gall position to vary. Unfortunately, stem mothers show such strong preferences for the leaf base that position varies little; 84% of the galls are positioned within the bottom 1 cm of the leaf blade (Whitham 1978). In spite of the low variation in gall positioning, comparisons of the extremes demonstrate the superiority of the basal gall site. Since mature galls measure ≈ 12 mm in length, solitary galls with their centers positioned 6–9 mm from the leaf base were used as the basal extreme, whereas the few solitary galls centered ≥ 18 mm from the leaf base were used as the distal extreme. An average of 65% more progeny were produced by solitary stem mothers positioned basally than by solitary stem mothers positioned distally (96.1 ± 6.97 progeny, $n = 132$; 58.4 ± 13.51 progeny, $n = 28$, respectively; $t = 2.306$, $df = 158$, $P < .025$). Since the average difference in position of these two extremes was only 18.6 mm, it appears small distances are important and account for the absence of galls on the distal two-thirds of the leaf blade.

These findings support the hypothesis that microhabitat differences within a leaf are responsible for positional differences in aphid success. In addition, the development rate of aphids is fastest at the leaf base (Whitham 1978), where phenolics are concurrently at their lowest concentrations (Zucker 1982).

DISCUSSION

This study addressed three major questions. First, with the removal of a competitor, does behavioral and reproductive release follow? Although there are numerous examples of experimentally determined behavioral release in birds (Hensley and Cope 1951, Stewart and Aldrich 1951, Watson 1967, Krebs 1971, Thompson 1977), fish (Gerking 1953, Fausch and White 1981), insects (Jacobs 1955, Baker 1972, Otte and Joern 1975, Davies 1978*b*, Wilson et al. 1978, Whitham 1979), mammals (Healey 1967, Smyth 1968, Krebs et al. 1976, Krebs 1978), and spiders (Riechert 1981), few studies have quantified the impact of behavioral release on reproduction. Stem mothers of *P. betae* released from competition show the following changes: (1) Probing and/or feeding behavior increases. (2) The remaining aphid crosses the dividing line that marked the former boundaries or territorial limits of both competitors. (3) The territory of the former competitor is incorporated into a new enlarged territory equal in size to the territory of a stem mother in the absence of competition. (4) Reproductive success significantly increases and equals the success achieved by stem mothers that occupied leaves singly from the onset of gall formation.

Second, what are the reproductive costs and benefits of territoriality? Brown (1964) introduced the concept of economic defendability in which there are predictable costs and benefits. The costs and benefits are usu-

ally measured in terms of energy (Smith 1968, Gill and Wolf 1975, Carpenter and MacMillen 1976, Kodric-Brown and Brown 1978), access to mates (Zimmerman 1971, Wiley 1973, Kitchen 1974, Floody and Arnold 1975) and predation or parasitism (Horn 1968, Krebs 1971, Caraco et al. 1980, Cade 1981, Martindale 1982, Dill 1983).

With *P. betae*, the costs and benefits have been directly quantified in terms of reproductive success. Solitary stem mothers achieve the highest reproductive success (100.7 and 142.2 progeny per attempted colonizer and surviving stem mother, respectively), followed by the basal stem mother of a competing pair (80.8 and 122.8, respectively), and then by the distal stem mother of a competing pair (51.7 and 88.8, respectively). The cost of losing in a competitive interaction is in part the difference in expected fitness for each of the above categories.

In holding leaf quality (i.e., size) constant to examine the effects of competitive release, the above estimates of the costs and benefits of territoriality are conservative. Superior leaves that result in 100% survival rates represent $< 1.6\%$ of the available leaves, while smaller leaves that result in 80% failure rates account for 32% of the tree's leaves (Whitham 1978, 1980). If by losing, a stem mother is forced to move to a smaller leaf, the costs of losing will be even greater.

When competitor densities are relatively high, the despotic behavior of the dominant stem mothers results in the formation of a floater population of subdominants that suffer high mortality. Whitham (1979) observed a 76% mortality rate for the floater population, compared to only 28% for the residents. When the resident stem mothers were physically removed, floaters moved into the vacated space. Resident stem mothers are often "tested" by new arrivals, which usually depart. Sometimes, after engaging in kicking–shoving contests, the resident may be displaced to the inferior distal position or from the leaf altogether.

As the stakes of winning or losing rise, contests of greater intensity and duration are more likely to occur (Mitchell 1980, Sigurjonsdottir and Parker 1981, Johnson 1982). Considering the price of failing in this system, it is not surprising contests may last 2 d and result in the death of one or both contestants (T. G. Whitham, *personal observation*). The term "aggressive neglect" in which aggression comes at the expense of some other important function such as food gathering (Ripley 1961, Brown 1971) may represent the necessary price paid to protect one's gall position and prevent displacement.

Third, how is "winning" in a territorial dispute affected by asymmetries in body size and what are the impacts on reproduction? Asymmetries in body size are known to be important in determining the outcomes of competitive interactions in diverse systems (Wilson 1975: table 13–2; Thornhill and Alcock 1983: table 9.1). The despotic behavior of large, solitary stem mothers acts to limit density on leaves where two stem

mothers could survive and reproduce, but at reduced levels. Smaller stem mothers are forced either to share leaves or settle on inferior, small leaves. Aoki and Makino (1982) also found body size to be important in determining the winner of competitive interactions of the gall aphid, *Epipemphigus niisimae*, and they observed that stem mothers were morphologically adapted for fighting.

Small differences in the body sizes of 1st-instar colonizing stem mothers are primarily related to dominance or competitive ability rather than reproduction. For example, an average difference of only 3.4% in the prothorax widths of stem mothers determined which ones occupied the superior gall sites. When released from the negative effects of competition, however, these same differences in body size had no effect on the subsequent production of progeny (i.e., $C = D = E$ in Fig. 1).

The advantages of large body size may have been important in contributing to a characteristic trait of the Erisomatidae, or gall-making aphids of which *Pemphigus* is a member. The stem mother is the "sole" offspring of a female sexual. The placing of all one's resources into a single egg that emerges in the spring as the stem mother is unusual. This life history trait, however, gives the largest stem mothers a competitive edge in a system where reproduction cannot be delayed until the next year, where smaller stem mothers forced to occupy inferior gall sites produce fewer progeny, and where despotic behavior results in a floater population of subdominants that suffer greater mortality.

The current examples of territoriality in aphids are restricted to gall aphids (Aoki 1978, 1979, 1980, Whitham 1979, Akimoto 1981, Aoki et al. 1981, Aoki and Makino 1982). *Pemphigus betae* gall aphids are presented with a highly heterogeneous host environment in which superior gall sites are relatively rare (Whitham 1981, 1983) and stem mothers compete for gall sites at even very low population densities (T. G. Whitham, *personal observation*). Furthermore, when stem mothers share the same leaf, induced leaf abscission greatly diminishes survival in comparison to solitary stem mothers (Williams and Whitham 1986). Acting in concert, these selection pressures may have favored the evolution of territoriality by these gall makers.

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