ogies of ovulate cones and pollen from the same species have responded to reproductive selective pressures incurred by anemophily. In this respect, wind pollination in the conifers appears to be a quite sophisticated and aerodynamically interactive system.

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2. Pollen impaction patterns for each species were determined by the point discharge of about 1000 pollen grains (determined by volume) 0.5 m from the ovulate cone target at varying wind velocities (0.5 to 10 m/sec) and orientations of the cones to airflow direction (normal, parallel, and at a 45° angle to flow). The scores for each species of ovulate cone were normalized on the basis of total impact number and surface area. Counts of pollen were determined by direct microscopic observation; see also (*5*).
3. Species are arranged in order of increasing pollen settling velocity. If only aerodynamic mechanism were involved, deposition efficiencies would be equal for different pollen species that have the same settling velocity for a given ovule target region. It appears from the data in Table 1 that aerodynamic mechanisms dominate; however, *P. rigida* and *P. strobus* should have the same percentages, but this was not observed (Table 1), implying that other net deposition mechanisms are important. Theoretically, the deposition percentage on the whole cone is expected to increase with pollen of greater settling velocities (and Stokes numbers). This trend was not always apparent (Table 1), indicating that nonaerodynamic mechanisms are significant in determining the observed species bias. The mechanisms involved in net deposition are impaction, rebound, rebound and reentrainment, and reentrainment, which are influenced by such factors as surface adhesion and roughness in addition to aerodynamic properties of the particles [K. T. Paw U, thesis, Yale University (1980); ——— and R. F. Reifsnyder, in *Proceedings of the 6th Conference on Fire and Forest Meterology*, Seattle, Washington, 22 to 24 April 1980, pp. 296–299].
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26 February 1982; revised 5 May 1982

Resource Partitioning and Interspecific Competition in Two Two-Species Insular *Anolis* Lizard Communities

Abstract. *Population experiments with* Anolis *lizard species demonstrate a relation between the amount of between-species competition and the degree of interspecific resource partitioning (the more the partitioning the less the competition). Specifically, the amount of resource partitioning between the two species (*Anolis gingivinus *and* Anolis wattsi pogus*) on the island of St. Maarten is less than that between the two species (*Anolis bimaculatus *and* Anolis wattsi schwartzi*) on the island of St. Eustatius. The presence of* Anolis wattsi *both lowers the growth rates and raises the perch heights of* Anolis gingivinus *individuals. In contrast,* Anolis wattsi *has no effect on* Anolis bimaculatus. *Thus, when there is less resource partitioning,* Anolis wattsi *has a greater competitive effect. This verifies, for these species, a central assumption of competition theory: the strength of between-species competition is inversely related to the amount of interspecific resource partitioning.*

Many studies in community ecology are based on the assumption that there is present-day competition between species and that the strength of the competition is inversely related to the degree of interspecific resource partitioning. However, few experimental studies demonstrate that interspecific competition exists, and few empirical studies of any kind attempt to determine how the strength of competition is related to the degree of interspecific resource partitioning. As a result, the theory of community ecology has been criticized (*1*). We now report results of density manipulation experiments designed to examine the above assumptions. The experiments involve two two-species *Anolis* lizard communities on islands in the Eastern Caribbean. These lizards are diurnal, insectivorous, and occur at high density (more than 10,000 per hectare). The species on the island of St. Maarten (*A. gingivinus* and *A. wattsi pogus*) are more similar in their resource use than the species on nearby (approximately 30 km) St. Eustatius (*A. bimaculatus* and *A. wattsi schwartzi*). Our data imply that competition between anole species is greater on St. Maarten than on St. Eustatius. We show that growth rates of *A. gingivinus* individuals are lower in the presence of *A. wattsi* than in their absence. Also, the presence of *A. wattsi* induces a shift in *A. gingivinus* resource use. No similar effects of *A. wattsi* on *A. bimaculatus* are observed. Thus, by these criteria, resource partitioning data correctly predict the rank order of the magnitude of interspecific competition.

Two locations, one on St. Maarten and one on St. Eustatius, were chosen for their similar topography [elevation, 150 to 200 m; 15° to 19° slopes facing northwest (310° to 339°), in ravines running northeast to southwest, on the northeast side of each island] and forest type (xeric, 6- to 8-m hardwoods with 2- to 3-m understory). Four enclosures (12 by 12 m) were constructed in each location during November, December, and January of 1980 to 1981. An enclosure consisted of a fence (1.15 m tall), embedded in the ground and topped with a polypropylene overhang. Also, a corridor, 2 m in width, on either side of the fence was cleared of vegetation to keep lizards from jumping over.

After construction, lizards were removed from the enclosures. The number of resident anoles captured in each enclosure (110 ± 7) represents an underestimate of the resident population size because some animals were removed with the vegetation that was cleared from the lanes. In December 1980 and January 1981 each area was restocked with animals caught outside that area. Two enclosures on St. Maarten (labeled GW1 and GW2) were each stocked with 60 *A. gingivinus* and 100 *A. wattsi pogus*. The other two St. Maarten areas (G1 and G2) were each stocked with 60 *A. gingivinus* and no *A. wattsi*. Similarly, two enclosures on St. Eustatius (BW1 and BW2) contained 60 *A. bimaculatus* and 100 *A. wattsi schwartzi* and two (B1 and B2) contained only 60 *A. bimaculatus*. The numbers and biomass of anoles introduced to the two-species enclosures were of the same order as population size and biomass estimates obtained in undisturbed sites (*2*). Introduced animals were permanently and individually marked by toe clipping. Size distributions and sex ratios (50:50) were carefully matched.

At monthly intervals, from January until May 1981, approximately 30 *A. bimaculatus* or *A. gingivinus* in each enclosure were recaptured, weighed, and measured. All unmarked animals were removed. These data were used to compute Lincoln estimates of population size. Three findings are indicated. First, we were successful in our original removal of lizards inasmuch as we never recovered more than four unmarked

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adults from any enclosure. Second, the fences were effective barriers to the dispersal of *A. gingivinus* and *A. wattsi* so that periodic restocking was unnecessary. However, *A. bimaculatus* areas required periodic restocking since the population sizes of these animals dropped to roughly half the initial value in 2 months' time. We believe that much of this decrease was due to emigration rather than predation. *Anolis bimaculatus* is the largest and most arboreal of the anoles studied, and marked individuals were occasionally captured outside the enclosures. Furthermore, the only known predator of anoles observed at the St. Eustatius sites, the pearly-eyed thrasher (*Margarops fuscatus*) (*3*), was actually observed more frequently at the St. Maarten sites. Third, we observed no significant effects of the presence of *A. wattsi* on the rates of lizard mortality or escape or hatchling production. This is, perhaps, not surprising as the experiment was of short duration and was performed during the dry season lull in anole breeding (*4*).

Resource use (niche position) was measured along four different resource axes (Table 1). The first axis is prey size which, in anoles, is monotonically related to body size (*5*). We confirmed this relation by dissecting anoles collected inside the enclosures at the end of the experiment (*6*). In that *A. bimaculatus* is larger than *A. gingivinus*, there is more interspecific partitioning of prey size on St. Eustatius than on St. Maarten. The remaining three resource axes are vertical space (perch height), activity time, and horizontal space. Horizontal space is divided into two categories, since there are two types of habitat within each enclosure—a denuded lane just inside the fence and a central forest patch. Niche position along these remaining axes was determined as follows. We spent two entire days, one in February and one in March, in each enclosure from an hour before dawn to an hour after dusk. At hourly intervals throughout the day we walked along a set path through the area. All lizards seen were classified according to species, perch height, and horizontal position. Care was taken not to record any lizard twice in one hourly walk. As with prey size, the partitioning of both vertical and horizontal space was greater on St. Eustatius than on St. Maarten (Table 1). No temporal partitioning was observed on either island. To summarize, there was more interspecific resource partitioning on St. Eustatius than on St. Maarten with respect to the three axes which were observed to be partitioned.

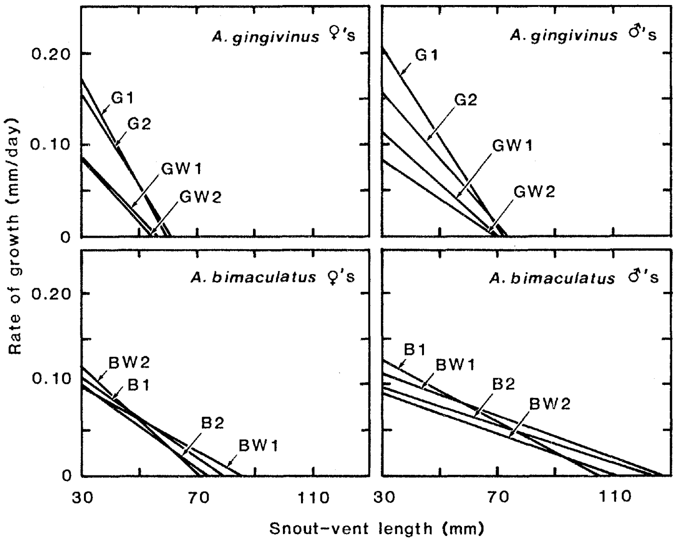

Fig. 1. Growth data linear regression analysis. Rate of growth (millimeters per day) on the *Y*-axis is regressed against length (millimeters) on the *X*-axis. Each line represents the "best fit" to a set of data points characterized by species, sex, and location (enclosure number). All slopes are significatly less than zero ($P < .01$, *t*-test). The sample sizes for each line range from 42 to 77.

We documented two effects of "treating" *A. gingivinus* populations with 100 *A. wattsi*. First, the presence of *A. wattsi*, a ground animal, resulted in significant ($P < .001$, Wilcoxon tests without tie correction) upward shifts in the mean perch heights of *A. gingivinus* (from 0.38 and 0.48 m in G1 and G2, respectively, to 0.89 and 0.87 m in GW1 and GW2). The presence of *A. wattsi* did not alter the mean perch heights of *A. bimaculatus*. There are no significant differences between the mean perch heights of *A. bimaculatus* in any two enclosures as indicated by Wilcoxon tests without tie correction.

The second observed between-treatment difference concerns the effect of *A. wattsi* on the growth rates of *A. gingivinus* individuals. Growth rates of *A. gingivinus* males and females when alone (in area G1 and G2) are approximately twice as high as when in the presence of 100 *A. wattsi* (in areas GW1 and GW2) (Fig. 1). All between-treatment differences in the growth rates of *A. gingivinus* are significant at the $P < .01$ level or higher (*7*). In contrast, there are no significant effects of *A. wattsi* on the growth rates of either male or female *A. bimaculatus* (*7*).

The insensitivity of *A. bimaculatus* growth rates to *A. wattsi*'s presence or absence is not due to complete inelasticity of the former's growth rate. We can, for example, detect an intraspecific effect of *A. bimaculatus* population size on the growth rates of both males and females. As was mentioned above, *A. bimaculatus* escaped from all enclosures at a rate such that after 1 month approximately 45 remained, and after 2 months approximately 30 remained, in each area. After partitioning the data, we observe that growth rates are significantly ($P < .01$) higher under conditions of low *A. bimaculatus* density (approximately 30 to 45) than under conditions of high *A. bimaculatus* density (approximately 45 to 60) (*7*).

Table 1. Resource use of the experimental species. Three resource axes are considered here: mean prey size as indexed by lizard size, perch height, and horizontal space. Horizontal space is divided into the two types of habitat found in each enclosure: denuded lanes and a forest patch. All differences except for comparisons of perch height of *A. wattsi pogus* and *A. wattsi schwartzi* are highly significant ($P < .001$). Perch height differences are tested by the Wilcoxon test with no tie correction. Horizontal space differences are tested via chi-square contingency tables.

Anolis species	Snout-vent length (mm)*	Perch height (m)*	*N*	Horizontal space		
				Denuded lane (%)	Forest (%)	*N*
		St. Maarten				
gingivinus	41.31 (7.69)	0.88 (0.80)†	440	41	59	1501
wattsi pogus	38.28 (3.52)	0.17 (0.09)	538	48	52	1029
		St. Eustatius				
bimaculatus	53.27 (12.58)	2.01 (1.71)	633	14	86	738
wattsi schwartzi	39.60 (5.31)	0.16 (0.17)	470	65	35	1340

*Mean (standard deviation). †Only data from areas GW1 and GW2 are used here because of the effect of *A. wattsi pogus* on *A. gingivinus*'s perch height. In all other cases, data from all four areas are pooled because there are no consistent differences between the treatments with and without *A. wattsi*.

We show that the degree of resource partitioning between *A. gingivinus* and *A. wattsi pogus* is greater than that between *A. bimaculatus* and *A. wattsi schwartzi* for the three axes along which we observe partitioning. The presence of *A. wattsi* results in both decreased growth rate and increased perch height for *A. gingivinus*. In contrast, no effects of *A. wattsi* on *A. bimaculatus* are observed. The resource partitioning data, therefore, correctly predict the relative strengths of *A. wattsi*'s competitive effect on the two larger *Anolis* species.

Because the *A. bimaculatus* population sizes decrease over time, the mean population density of enclosed *A. bimaculatus* is less than the mean density of enclosed *A. gingivinus*. Another interpretation of our results might be that we observe less competition on St. Eustatius only because of the lower mean population size of animals there. Our data, however, do not support this interpretation. We may partition the St. Eustatius growth and resource use data as before into two classes, one for high *A. bimaculatus* population density (60 to 45) and one for low *A. bimaculatus* density (45 to 30). In the high density class, the mean population size of *A. bimaculatus* (52 per enclosure) is not appreciably lower than the mean population size of *A. gingivinus* (55 per enclosure), and the biomass of *A. bimaculatus* per enclosure is actually higher than the biomass of *A. gingivinus*. Nonetheless, there are no effects of the presence of *A. wattsi* on the growth rate or perch height of *A. bimaculatus* at either high or low *A. bimaculatus* density [Wilcoxon tests without tie correction (*7*)].

Although we have concentrated on the effects of the smaller *Anolis* species on individuals of the larger species, we anticipate that we would obtain similar results from a study of the effects of the two larger species on *A. wattsi*. On St. Maarten it appears that *A. gingivinus* excludes *A. wattsi* from lowland locations, whereas on St. Eustatius *A. wattsi* distribution does extend to sea level. In introduction experiments on an offshore cay near St. Maarten we, together with J. Rummel, have shown that *A. gingivinus* reduces the survivorship of *A. wattsi* in sea-level habitat (*2*). We also show that *A. wattsi* adults can survive for more than 2 years and reproduce in the sea-level habitat. These results suggest that the absence of *A. wattsi* from sea-level habitat on St. Maarten is caused by an interaction with *A. gingivinus* and not by any serious unsuitability of the lowland habitat for *A. wattsi*. In contrast, the extension of *A. wattsi*'s range to sea level on St. Eustatius suggests a weaker effect of *A. bimaculatus* on *A. wattsi*.

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7. We use the following procedure to test for statistically significant differences between growth rate distributions. First, we test for differences among the size distributions of animals from which the growth data were taken. All size distributions for each sex and species are statistically indistinguishable (Wilcoxon tests with tie correction). We then test for differences between the growth rate distributions (ignoring body size) with Wilcoxon tests (without tie correction).
8. Supported by NIH graduate traineeship GM7181-05 and NSF grant 2FAA-469-94647. We thank Mayor Elie Fleming of French St. Martin and the government of St. Eustatius for the use of the study sites; S. Adolph, J. Rummel, E. Kauzmann, and P. Kauzmann for field assistance. Special thanks to K. E. Kauzmann Pacala for fieldwork and support during all phases of the work.

21 December 1981; revised 5 May 1982

Manipulations of Endosperm Balance Number Overcome Crossing Barriers Between Diploid *Solanum* Species

Abstract. *Abortion of the hybrid endosperm is the basis for the inability to hybridize many angiosperm species. This has made it nearly impossible to incorporate the valuable characteristics from several wild, diploid* Solanum *species into the cultivated potato* Solanum tuberosum. *But some wild species have "endosperm balance numbers" different from those of most* Solanum *diploid species, and these numbers or "effective ploidies" can be manipulated to create new hybrids.*

Endosperm, a tissue peculiar to angiosperms, is formed by the fertilization of the central cell of the embryo sac by a sperm identical to the one which fertilizes the egg. The endosperm is triploid (3x) in crosses between diploids (2x × 2x) since it receives two sets of maternal chromosomes and one set of paternal chromosomes. After fertilization, the endosperm grows rapidly, becoming the nutritive tissue for the embryo. The nature of the endosperm ranges from an ephemeral tissue, as in bean, to a major tissue in the mature seed, as in corn. However, in almost all angiosperms the survival of the embryo is dependent on the normal development of the endosperm (*1*). Therefore, endosperm is important not only as the major food stuff of man and his livestock, but also because its normal development is necessary to support the development of a viable embryo, thus placing a restraint on our ability to genetically improve crops through sexual hybridization. This limitation is especially important in efforts to introduce into cultivated lines valuable characteristics from wild and exotic germplasm.

There are several types of endosperm dysfunction which prevent crossing (*1*). One type is evident in intraspecific, interploidy crosses. For example, crosses between a diploid and its colchicine-induced tetraploid form generally fail because the endosperm aborts. The cause of this type of dysfunction has been a source of experimentation and debate for over 50 years (*2*). Lin (*3*) clarified the problem by demonstrating that in corn a 2:1 ratio of maternal:paternal chromosomes is necessary for normal endosperm development. In a 2x × 4x cross the maternal:paternal chromosome ratio in the endosperm would be 2:2 and in a 4x × 2x cross, 4:1.

The 2:1 ratio rule is applicable to most intraspecific and many interspecific crosses. However, there are many interspecific crosses whose endosperm development does not conform to the 2:1 ratio rule (*2*). For example, 4x (2n = 4x = 48) *Solanum acaule* yields aborted seed when crossed with the cultivated potato, 4x *S. tuberosum* Group Tuberosum. Yet, *S. acaule* crosses readily with 2x (2n = 2x = 24) haploids extracted from Gp. Tuberosum, producing seeds with normally developed endosperm (*4*). In the 4x *S. acaule* × 4x Gp. Tuberosum cross, the maternal:paternal ploidy ratio in the endosperm is 4:2 (=2:1), yet the endosperm aborts, while it develops normally in the 4x *S. acaule* × 2x Gp. Tuberosum haploid cross where the maternal:paternal ploidy ratio is 4:1.

An "endosperm balance number" (EBN) hypothesis has been proposed (*2*)

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