

REPORT

Testing intraguild predation theory in a field system: does numerical dominance shift along a gradient of productivity?

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Abstract

Although ecological theory exists to predict dynamics in communities with intraguild predation (IGP), few empirical tests have examined this theory. IGP theory, in particular, predicts that when two competitors interact via IGP, with increasing resource productivity: (1) the IG predator will increase in abundance as the IG prey declines, and (2) increasing dominance of the IG predator will cause resource density to increase. Here, we provide a first test of these predictions in a field community consisting of a scale insect and its two specialist parasitoids, *Aphytis melinus* (the IG predator) and *Encarsia perniciosi* (the IG prey). The shared resource, California red scale, is a pest of citrus, and its productivity varies across a threefold range among citrus cultivars. We examined both absolute and relative densities of parasitoids along this natural gradient of scale productivity in three citrus cultivars (orange, grapefruit and lemon). Although both parasitoid species were found in all three cultivars, their abundances reflected those predicted by IGP theory: the IG prey species dominated at low productivity and the IG predator dominated at high productivity. This relationship was caused by an increase in *Aphytis* density with productivity. In addition, the density of scale increased with the dominance of the IG predator. These results from a field system demonstrate the important dynamic outcomes for food webs with IGP.

Keywords

Aphytis melinus, California red scale, community theory, *Encarsia perniciosi*, food web, trophic interactions.

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INTRODUCTION

Intraguild predation (IGP), predation on a consumer species by its guild member, is common in natural communities (Polis *et al.* 1989) and has received substantial attention in the theoretical literature, particularly following the recent publication of a general theory of IGP by Holt & Polis (1997). The theory has shown that the presence of IGP in a community has implications for important ecological issues including the relationship between food web stability and diversity, coexistence of resource competitors, suppression of the shared resource and effects of productivity on trophic interactions. The most consistent prediction from all formulations of IGP theory is a unimodal species diversity–productivity relationship (Diehl & Feissel 2001). In the region of coexistence, IGP theory predicts that, with increasing resource productivity, the IG predator will

increase in abundance relative to the IG prey species, causing an increase in resource density.

Although the IGP relationship between species diversity and resource productivity has been examined theoretically, there are few empirical tests. However, four notable exceptions exist (Morin 1999; Amarasekare 2000; Diehl & Feissel 2000, 2001). Three of these studies were performed with protists competing for bacterial resources in laboratory microcosms, and were able to reproduce the IGP theoretical prediction of the IG prey alone persisting at low resources, and coexistence of the IG predator and IG prey at intermediate resources. One study also found extirpation of the IG prey at high resource levels (Diehl & Feissel 2000). In the only field study examining these predictions, Amarasekare (2000) showed that the IG predator, a parasitoid (*Trissolcus murgantiae*), could not persist in low productivity patches of the resource

(a harlequin bug, *Murgantia histrionica*); however, the IG prey (also a parasitoid, *Ooencyrtus johnsonii*) and IG predator coexisted in more productive resource patches. No field study to date has explicitly examined the IGP prediction of increasing relative abundance of the IG predator within the coexistence region, or has any field experiment examined the relationship between IG predator dominance and resource density. In this study, we examine the abundance patterns of two parasitoids and their shared host within the region of coexistence in a field community with IGP.

California red scale (*Aonidiella aurantii*), a pest of citrus crops present worldwide, has been maintained under successful biological control by its parasitoids in California for over half a century (DeBach *et al.* 1971). The densities of both host and parasitoids in this field community are extremely temporally stable (Murdoch 1994), thereby meeting the important assumption in IGP theory of a community at equilibrium. In addition, two parasitoid wasps, *Aphytis melinus* and *Encarsia perniciosi*, coexist on California red scale in coastal California citrus groves and interact via IGP. While other parasitoid species attack red scale in these groves, they are present only in extremely low abundances. The interaction between *Aphytis* and *Encarsia* has been studied both empirically (Yu *et al.* 1990; Borer 2002a) and theoretically (Borer 2002b). In this interaction, *Encarsia* an endoparasite and obligate primary parasitoid of red scale, acts as the IG prey. Empirical evidence suggests that *Encarsia* is superior to *Aphytis* in exploiting the red scale (Borer *et al.* in press; DeBach & Sundby 1963). *Aphytis*, an ectoparasite and facultative hyperparasitoid, successfully attacks both unparasitized hosts as well as hosts already containing developing *Encarsia* juveniles, thereby making it the IG predator.

Work in this system has also shown that California red scale productivity (i.e. fecundity) varies among citrus cultivars, creating a natural gradient of pest productivity for testing IGP predictions. For example, Hare *et al.* (1990) showed that red scale insects on grapefruit have a low initial egg complement, while scale insects on lemon have a high initial egg complement.

Thus, California red scale insects exist in equilibrium in field populations with a gradient of resource productivity in

which two coexisting resource competitors interact via IGP. Therefore, this community provides an excellent system to examine the densities of the IG predator and IG prey species, and the resulting red scale density across a gradient of resource productivity as a test of IGP theory. In this study, we focus on two predictions of IGP theory: (1) the IG predator density should increase relative to the IG prey density with increasing resource productivity, and (2) the resulting densities of California red scale should increase with increasing abundance of the IG predator.

AN ILLUSTRATIVE MODEL

The predictions about the effects of resource productivity on the outcome of IGP are illustrated by the model presented in Table 1 and Fig. 1. This model is a simple variant of the IGP model thoroughly analysed by Holt & Polis (1997). Although it is an extremely simplified caricature of our real community, it illustrates the theoretical predictions common to all models of IGP in which a three-species equilibrium exists. The only feature of the Holt and Polis model that we have altered is that the logistic growth rate of the resource in the absence of predation has been changed to an equivalent formulation separating the processes of births and deaths, with the density dependence occurring only in the per capita death rate. This does not alter the model results, but allows us to plot our results in terms of the resource birth rate (the parameter for which we have estimates in our system) rather than the resource carrying capacity, while maintaining a simple formulation. While a three-species equilibrium is not a necessary outcome of this model (Holt & Polis 1997), we focus on this region of parameter space in the current context.

We present this model to illustrate the general predictions of the effects of increasing productivity in IGP systems and not to examine a specific representation of the California red scale system. Including numerous biological details found in the California red scale system (stage structure, host feeding, invulnerability, resource availability, etc.) does not alter the general IGP predictions we focus here (Briggs 1993; Borer 2002b).

The equilibrium predictions of the IGP model in Table 1 are shown in Fig. 1. If the productivity of the shared

Table 1 Formulation of a simple intraguild predation model based on a model by Holt & Polis (1997)

$$dH/dt = rH - a_pHP - a_QHQ - H(d_H + qH)$$

$$dP/dt = c_p a_p HP - d'_Q PQ - d_p P$$

$$dQ/dt = c_Q a_Q HQ + c'_Q d'_Q PQ - d_Q Q$$

where H , herbivore density; P , intraguild prey (IG prey) density; Q , IG predator density; r , herbivore birth rate; a_p , IG prey feeding rate on the herbivore; a_Q , IG prey feeding rate on the herbivore; d'_Q , IG prey feeding rate on IG prey; c_p , IG prey conversion efficiency on the herbivore; c_Q , IG prey conversion efficiency on the herbivore; c'_Q , IG prey conversion efficiency on IG prey; d_H , herbivore death rate; d_p , IG prey death rate; d_Q , IG prey death rate; and q , strength of density dependence in herbivore death rate.

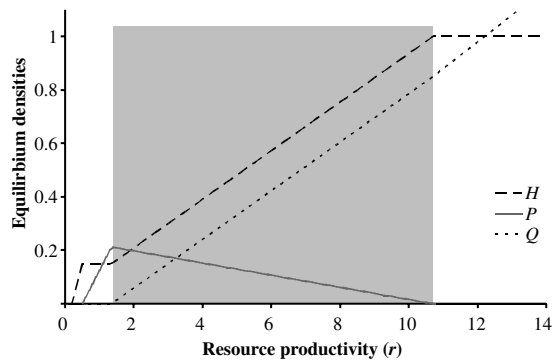


Figure 1 An example of the effects of increasing resource productivity, as measured by r , the birth rate of the resource, on the equilibrium densities of intraguild (IG) predator, IG prey and resource. Coexistence of the IG prey and IG predator is possible only in the shaded region and can occur only if the IG prey is the superior exploitative competitor for the shared resource. The resource equilibrium (H, dashed line) increases with increasing birth rate (productivity). Because the IG predator (Q, dotted line) is the poorer resource exploiter, as the IG predator increases relative to IG prey (P, grey line), the resource equilibrium also increases because of a release from top-down control. Within the region of guild member coexistence, with increasing resource productivity, the IG predator increases in relative abundance to the IG prey. With increasing r , the equilibrium density of the IG predator increases with a steeper slope than that at which the IG prey decreases whenever $a_P c_P > a_Q c_Q / c'_Q$. This condition is always true whenever the parasitoids coexist. Parameter values for equilibria are: $a_P = 4$, $a_Q = 10$, $d'_Q = 2$, $c_P = 0.5$, $c_Q = 0.1$, $c'_Q = 2$, $d_P = 0.3$, $d_Q = 1$, $d_H = 0.1$ and $q = 2$. These values are illustrative and do not represent estimates for the California red scale system. For equations describing system dynamics, see Table 1.

resource is extremely low, neither IG prey nor IG predator can persist on the resource (Fig. 1; $r < 0.5$). If the IG predator and IG prey coexist under any conditions, the IG prey must be the better exploiter of the basal resource. Therefore, with a small increase in the productivity of the basal resource, the IG prey can invade (Fig. 1; $r \cong 0.5$). As the IG predator uses the IG prey as a second resource, an increase in basal resource productivity that increases the IG prey equilibrium density allows invasion by the IG predator (Fig. 1, shaded region). When all three species are present, the equilibrium density of the basal resource increases with system productivity, and the densities of the IG predator and IG prey shift increasingly to favour the IG predator. Finally, at high productivity, species diversity declines again because the IG predator extirpates the IG prey and persists at equilibrium only on the basal resource (Fig. 1; $r > 10.5$).

In addition, we note here that within the region of three-species coexistence, the IG predator equilibrium density increases with increasing productivity more rapidly than the IG prey equilibrium density declines. In the current

formulation, the density of each predator species changes linearly with increasing r . It can be shown that the slope at which the IG predator equilibrium increases with increasing r is steeper than the slope at which the IG prey equilibrium decreases, whenever $a_P c_P > a_Q c_Q / c'_Q$. This condition is true whenever the parasitoids coexist. Although the shape of the relationship between the IG predator and IG prey equilibria and resource productivity is not linear in all IGP formulations, particularly those involving density dependence in the resource growth rate (e.g. Holt & Polis 1997), the qualitative pattern that the IG predator density increases more rapidly than the IG prey density decreases appear to be general.

METHODS

We combined (1) data on parasitoid densities in three citrus cultivars, collected in the fall of 1989 with (2) data on California red scale productivity (Hare *et al.* 1990) to examine a gradient of resource productivity, whether host and parasitoid densities followed those predicted by IGP theory.

Parasitoid abundance and scale density

All 12 groves sampled in this study were located near Fillmore, CA, USA. In October and November 1989, we collected 20–40 twigs from eight randomly chosen trees in four replicate groves of three citrus cultivars: lemon (*Citrus limon*), sweet orange (*C. sinensis*) and grapefruit (*C. paradisi*). In this study, a 'twig' represented the stems of the four newest flushes of tree growth (leaves were not sampled). We transported the twigs back to the laboratory and stored them in a cooler at 4 °C. We examined and counted all scale insects on stems under a microscope, recorded the stage of each scale, and measured the total stem area for each twig. If a scale was parasitized, we also recorded whether it contained an *Encarsia* or other endoparasitoid pupa or *Aphytis melinus* (an ectoparasitoid). Other data collected on citrus suggest that *E. perniciosi* comprised ca. 90% of the endoparasitoids in our samples (R. Luck, D. S. Yu, W. Murdoch & S. Walde, unpublished data). However, IGP is a general interaction between endoparasitoids (IG prey) and ectoparasitoids (IG predators) (Flanders 1971; Godfray 1994), therefore, we examined our data with only *Aphytis* and *Encarsia* and again with all endoparasitoids included. Here, we present the results including only *Encarsia*; however, our results were virtually identical with all endoparasitoids included.

Scale productivity

Hare *et al.* (1990) published life-history parameters for California red scale on four citrus cultivars: lemon,

grapefruit, mandarin (*C. unshiu*) and sweet orange. In this study, initial egg complement of gravid female red scales, a measure of scale productivity, was measured in three seasons (spring, summer and autumn). The ranking of scale productivity in Hare *et al.* (1990) was variable among seasons, but was not measured in replicate years; however, data from Carroll & Luck (1984) suggest that, at least in navel oranges, interannual variability in red scale egg complement is quite low. To minimize any error caused by seasonal differences in egg production on the three cultivars, we compared our field data with their September data (Hare *et al.* 1990), because this was the season when we collected parasitoid abundance and scale density data. In their September sample, Hare *et al.* (1990) found that the initial red scale egg complement was significantly different among cultivars. Initial egg complement was highest on leaves of lemon (42.35), intermediate on leaves of orange (32.71) and lowest on grapefruit leaves (15.53). In addition, scale survival from settlement to adult was not different among cultivars in the field (Hare *et al.* 1990).

Our data provide confirmation that a comparison between our field parasitism rates and Hare *et al.*'s (1990) September red scale productivity data is appropriate. Although we did not directly measure red scale productivity during our field surveys (e.g. as initial egg complement), a surrogate for productivity calculated from our data mirrored Hare *et al.*'s (1990) autumn ranking among cultivars. We estimated red scale productivity from our data set as the number of youngest juvenile scale (first instars) divided by the number of mature and reproductive (crawler producing) red scale females. The mean for this metric of red scale productivity was highest in lemon groves (7.97 ± 2.6 SE) and slightly higher in orange (4.38 ± 2.90 SE) than grapefruit groves (4.29 ± 0.62 SE). As California red scale is under good control in all cultivars, mature females and crawler-producing females are rare in randomized field surveys. For example, in our samples from nine of 12 groves, we found less than five crawler-producing females and <25 mature and crawler-producing females. Thus, the estimate provided by our field data, while in qualitative agreement with Hare *et al.*'s data, had high variance because of low sample sizes. Because of the qualitative agreement between our data set and Hare *et al.*'s published data, and as the data provide a more appropriate empirical estimate of the model parameter of interest (red scale per capita productivity), we therefore use the estimates of productivity provided by Hare *et al.* (1990). However, we note here that the results of our analyses using a rank ordering of cultivar productivity, our field surrogate for cultivar productivity, or Hare *et al.*'s productivity measurements resulted in the same qualitative outcome for this study (i.e. slope direction and significance).

In addition, although productivity data were collected by Hare *et al.* (1990) on leaves while our data were collected on

stems of citrus trees, further evidence suggests that this is an acceptable comparison. In a study on navel oranges, Carroll & Luck (1984) showed that the number of eggs produced by California red scale is remarkably consistent across substrates, confirming that a comparison of parasitoid density on stems with red scale egg production on leaves is appropriate and meaningful. Thus, in the current study we compare Hare *et al.*'s (1990) initial egg complement data, a surrogate for scale productivity, with our field surveys of parasitoids and scale.

Statistical methods

We used logistic regression to determine whether there was a change in the relative abundance of *Aphytis* to total parasitism among cultivars. We included in our analysis only parasitized hosts containing parasitoid pupae, and calculated the total number of *Aphytis* and *Encarsia* pupae found in each of the 12 study groves. In this model, $Y \sim \text{binomial}(p)$ and $\ln[p_i/(1 - p_i)] = \beta_0 + \beta_1 C$, where p_i is the conditional probability that a parasitized scale from a given cultivar will be parasitized by *Aphytis*. C represents the cultivar productivity and takes on values of 15.53 (grapefruit), 32.71 (orange), or 42.35 (lemon), following Hare *et al.* (1990).

We examined the density of each parasitoid in each cultivar by dividing the total number of parasitoids in a grove by the total twig area sampled in that grove. In this analysis, we used the log of the parasitoid density as our response variable to normalize the residuals. We did a simple linear regression on this transformed variable to determine whether $\log_{10}(\text{density})$ could be predicted by cultivar productivity. Cultivar productivity took on the same values as in the parasitism analysis.

The density of scale across cultivars was examined to determine whether this increased with increasing dominance of the IG predator. We used the same methods as outlined for parasitoid density to calculate scale density in each grove and employed the log of density in a simple linear regression, as for parasitoid density. Cultivar productivity took on the same values as in the parasitism analysis. Finally, in a multiple regression model, we used the log-transformed density variables to assess the relationship between red scale density and the densities of *Aphytis* and *Encarsia*. All analyses were performed in SAS (SAS Institute, Cary, NC, USA).

RESULTS

Both parasitoids were found in all groves of the study; however, along an increasing gradient of California red scale productivity among cultivars (Hare *et al.* 1990), the mean percentage of *Aphytis* density to total parasitoid density increased from 10.3 to 44.7% ($P < 0.0001$). An analysis of the density of each parasitoid demonstrated that the increase

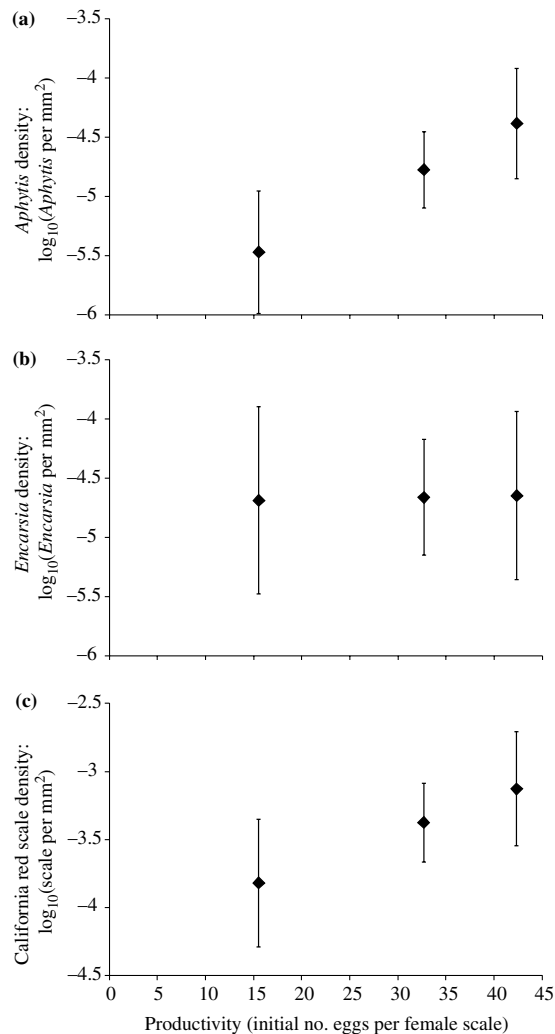


Figure 2 The pattern of intraguild (IG) predator, IG prey and red scale density are consistent with IGP predation theory. (a) Density of *Aphytis* increases with increasing initial egg complement of female red scale, a proxy for scale productivity. The estimated linear regression model for *Aphytis* density is: $\log_{10}(\text{Aphytis per mm}^2) = -6.10 + 0.041 * \text{cultivar productivity}$. (b) The density of *Encarsia* does not increase significantly with increasing red scale productivity. The estimated regression model for *Encarsia* density is: $\log_{10}(\text{Encarsia per mm}^2) = -4.71 + 0.001 * \text{cultivar productivity}$. (c) Density of California red scale increases with increasing cultivar productivity. The estimated linear regression model is: $\log_{10}(\text{scale insects per mm}^2) = -4.22 + 0.026 * \text{cultivar productivity}$. Error bars for all panels represent the 95% confidence interval for each regression model.

in the percentage of *Aphytis* was driven by an increase in *Aphytis* density with increasing cultivar productivity (Fig. 2a; $P = 0.0095$) combined with no discernible change in *Encarsia* density (Fig. 2b; $P = 0.9412$). The increasing dominance of *Aphytis* in our empirical observations followed

the pattern of relative IG predator density predicted by IGP theory within the region of coexistence (Fig. 1), although the lack of trend in *Encarsia* density did not match the predicted decline in the IG prey density with increasing resource productivity.

Scale density increased with increasing scale productivity among cultivars (Fig. 2c; $P = 0.0480$). This followed IGP theory, which predicts that resource density should increase with productivity (Fig. 1).

Finally, we analysed the relationship between scale density and the density of each parasitoid. Among groves, scale density was positively related to *Aphytis* density ($P < 0.0001$), but unrelated to *Encarsia* density ($P = 0.2709$). Within the region of coexistence, the rapid increase in resource density was associated with increasing IG predator density, as predicted by IGP theory (Fig. 1).

DISCUSSION

The abundance of *Aphytis* increased relative to *Encarsia* more than threefold among three citrus cultivars along an increasing gradient in resource (scale) productivity. This pattern of increasing IG predator relative to IG prey abundance was driven by an increase in the IG predator with no discernible change in the IG prey density. The increase in IG predator density followed IGP theory, while the theoretical expectation of decreasing IG prey density was not fulfilled. The pattern of increasing scale density with increasing cultivar productivity also reflected the predictions of IGP theory. In addition, our data agree with the prediction that IG predator density should increase more rapidly than the IG prey density declines. These results represent the first tests in a field system of these predictions from IGP equilibrium theory.

Other published field data corroborate and extend our results linking field observations of red scale density to IGP theory. Cameron *et al.* (1969, 1975) and Habib *et al.* (1972) sampled scale infestations of several cultivars of citrus and found that lemon always supported the highest red scale populations while orange always supported smaller populations. Grapefruit was variable among studies. IGP theory predicts that at high resource productivity, the IG predator should be numerically dominant (Holt & Polis 1997; Diehl & Feissel 2000). As the IG predator is less efficient at resource exploitation, the basal resource equilibrium should increase with this reduction in top-down control of the resource. Therefore, several studies corroborate our results showing that the observed red scale (resource) densities reflect those predicted by IGP theory for this system in which the red scale predators interact via IGP.

However, alternative explanations for these patterns are possible. *Aphytis* preferentially attacks red scale on leaves (Borer *et al.* in press), therefore if the ratio of stem to leaf

differs among cultivars, parasitoid density may be determined by structural differences rather than direct species interactions. For substrate ratios to explain the observed pattern, lemon trees should have substantially more leaf area relative to stem area compared with grapefruit. While growth patterns appear similar among citrus cultivars, the ratio of these substrates has never been quantified. Another possible explanation is that cultivars may not support the same suite of predators (e.g. generalist beetles), thus the observed pattern may have been derived from a mechanism such as apparent competition. However, our observations in orange, lemon and grapefruit groves suggest that species composition is very similar among cultivars. In addition, evidence suggests that generalist predators do not have substantial impacts on the population dynamics of the parasitoids of California red scale (DeBach 1958).

The IGP theory predicts that at very low or high productivity the IG prey or IG predator (respectively) should persist alone with the resource (Holt & Polis 1997). The formulation of the IGP model used here was an extremely simplified caricature of the real interaction; however, the productivity–density relationships predicted by IGP theory are general and hold even in far more complex, system-specific models (Briggs 1993; Borer 2002b). As both species were found in all cultivars, our data suggest that California red scale may not have a broad range of productivity among cultivars to cause extinction of either consumer species. In fact, there is no cultivar of which we are aware in which these species do not coexist. Thus, the theoretical predictions for community structure at the extremes of productivity may be better examined in a field system in which resource productivity (e.g. fecundity) can be directly manipulated.

Within the range of resource productivity examined in this study, we found that *Aphytis* density increased with productivity, but was coupled with no discernible shift in *Encarsia* density. The theory predicts that the IG prey density should decline more slowly than the IG predator density increases in the region of three-species coexistence, so the absence of a trend in the density of *Encarsia* may simply reflect our inability to detect this shallow declining slope of the species. Alternately, *Encarsia* may be retained in the system at high productivity because of other mechanisms acting in the system. For example, although IGP may be the primary mechanism driving the observed density patterns of parasitoids, multiple mechanisms of coexistence could be operating in this system (Borer *et al.* in press). However, along the natural gradient of red scale productivity examined in the current study, we did find the predicted shift in relative species abundance within the region of coexistence.

Although many past studies have purported to test IGP theory, most do not meet the criterion of equilibrium required for appropriate tests of the theory. Transient

dynamics can persist for decades or longer depending on model parameter values (Hastings & Higgins 1994), therefore, imposed initial species densities, particularly in short-term field manipulations, do not provide adequate tests of IGP theory. This is the first test of IGP theory within the region of coexistence in an equilibrium field system, and we found that the relative abundances of IG predator and IG prey and the resulting red scale density followed the pattern predicted by the theory.

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