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Thomas J. Valone; James H. Brown

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- previous year's shrub shoots is not included in our estimates.
21. For forbs, $AGB = LAI \times (49.94 \pm 4.76) \text{ g/m}^2$ ($N = 10$) and $AGB = (\text{percent of areal coverage}) \times 2.79 \text{ g/m}^2$ ($N = 10$). For graminoids, $AGB = LAI \times (26.20 \pm 2.34) \text{ g/m}^2$ ($N = 10$) and $AGB = (\text{percent of areal coverage}) \times (2.19 \pm 0.23) \text{ g/m}^2$ ($N = 10$). For shrubs, incremental $AGB = (\text{incremental shoot length in centimeters per square meter}) \times (0.028 \pm 0.005) \text{ g/m}^2$ ($N = 19$), and incremental shoot length = $(\text{percent of areal coverage}) \times (171.8 \pm 11.3) \text{ cm/m}^2$ ($N = 10$). Regressions of LAI or shoot length against the direct measure of AGB carried out separately for each zone and for each treatment showed no significant dependence of regression coefficients on zone or treatment.
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24. The need to consider the climate sensitivity of all life stages of vegetation is emphasized by F. I. Woodward and B. G. Williams [*Vegetatio* **69**, 189 (1987)].
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26. M. S. Kearney and B. H. Luckman, *Science* **221**, 261 (1983). Although we did not find a Quaternary record specifically from the western Rocky Mountains, the evidence cited is from other regions within the Cordillera.
27. The importance of reliable forecasts of interannual climatic variability is underscored by our observation that the magnitude of the effect of heating on AGB varied with summer soil moisture levels; see also (23) and N. L. Stephenson, *Am. Nat.* **135**, 649 (1990).
28. Investigation of climate controls on growth of tundra species shows that within the broad grouping of forbs or shrubs, species at a particular site can differ

- markedly in their responses to environmental influences (22).
29. We thank C. Still and L. Tucker for assistance with fieldwork and N. Arens for her help in understanding the Quaternary pollen record. We also thank M. Loik, M. Price, and N. Waser for advice, C. D'Antonio, J. Dunne, S. Hobbie, A. Kinzig, M. Loik, S. Saleska, K. Shen, M. Torn, and M. DeLapa for editorial comments, and the staff of RMBL for support. This work was supported by grants from the National Science Foundation (DEB-9207588 and BSR-9020579), the U.S. Department of Agriculture's Cooperative State Research Service (CA-B*-SSC-5113-H), the Pew Charitable Trusts, by a predoctoral fellowship from the U.S. National Aeronautics and Space Administration, and by a John Simon Guggenheim Foundation fellowship.

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Effects of Competition, Colonization, and Extinction on Rodent Species Diversity

Thomas J. Valone*† and James H. Brown

Analyses of long-term experimental data from the Chihuahuan desert revealed that species diversity of other rodents was higher on plots from which kangaroo rats (*Dipodomys* spp.) had been removed. The difference was due to consistently higher colonization and lower extinction probabilities of small granivorous rodents in the absence of competitively dominant kangaroo rats. The results of this ecosystem experiment demonstrate the importance of both competitive exclusion and metapopulation dynamics for biological diversity in a natural community.

Theoretical and laboratory studies suggest that the number of species that coexist in a community is influenced by several processes, including competition, predation, mutualism, disturbance, and physical stress (1–6). Although there is evidence that each of these factors can affect the relative abundance of species in a natural community, there are few examples of how, either singly or in combination, they affect the number of coexisting species. Further, in order for these processes to alter species diversity rather than just relative abundance, they must affect metapopulation dynamics; that is, the probabilities of local colonization and extinction (6–8).

Mathematical models predict, and laboratory experiments have demonstrated, competitive exclusion—the capacity of a competitor to cause the local extinction of another species (1, 9). Evidence for competitive exclusion from field studies is more equivocal (4, 10–13). Examples of extinction of species native to islands and other isolated habitats are difficult to explain solely by competition from invading exotics, because such extinctions almost always coin-

cide with increased human influence (14).

Here we demonstrate the effect of competition on species diversity in a community of rodents in the Chihuahuan desert. The removal of seed-eating kangaroo rats (*Dipodomys* spp.) from small experimental plots increased the number of small granivorous rodent species. These increases in diversity resulted from higher probabilities of colonization or lower probabilities of extinction, or both.

In 1977, experimental plots (50 by 50 m) were established on a 20-ha site of relatively homogeneous Chihuahuan desert scrub vegetation near Portal, Arizona. Each plot was surrounded by wire mesh topped with aluminum flashing to control access by rodents. Plots were assigned various experimental treatments that included exclusion of different rodent species on the basis of body size. Equal access (or control) plots had 16 large (3.7 by 5.7 cm) gates in the wire mesh, which allowed access to all rodents. Plots from which kangaroo rats were removed had 16 small (1.9 by 1.9 cm) gates in the wire mesh, which allowed access by all small-bodied rodents but prevented the larger bodied kangaroo rats (*Dipodomys spectabilis*, *D. merriami*, and *D. ordii*) from entering. From 1977 to 1987, there were 14 equal access and 4 kangaroo rat removal plots. In 1988, some equal access plots were converted into new kangaroo rat removal plots by changing their

gate size. Thus, from 1988 to the present (March 1994), there were eight equal access plots, four old kangaroo rat removal plots (*Dipodomys* excluded continuously since 1977), and four new kangaroo rat removal plots (*Dipodomys* excluded continuously since 1988).

Approximately each month since 1977, rodents on all plots have been censused. For one night, 49 Sherman live traps were placed on each plot and baited with millet. During each census, all gates were closed so that only resident individuals were caught. All individuals captured were identified, measured, uniquely marked, and released (13).

Kangaroo rats compete strongly with other rodents (15) and have large effects on vegetation (16, 17). Within 1 to 2 years of removal of kangaroo rats from experimental plots, densities of small seed-eating rodents increased more than twofold (13, 15); 8 to 10 years after kangaroo rat removal, annual and perennial grass density increased more than threefold (16, 17).

Species diversity of the other nocturnal rodents changed in response to experimental removal of kangaroo rats. During the past 17 years, a total of 14 such species have been recorded. Kangaroo rat removal plots usually supported more species of other rodents than did equal access plots (Fig. 1).

From 1977 to 1981, there was no difference in the number of non-*Dipodomys* species caught per month between equal access and kangaroo rat removal plots (Table 1). From 1982 to 1987, and again from 1988 to 1994, however, there were more rodent species per month on kangaroo rat removal plots than on equal access plots (Table 1). The increasing trend in species diversity can be attributed, in part, to the indirect effect of kangaroo rats on rodents through vegetation (18, 19), as well as to the direct effect of the relaxation of competition.

From 1982 to 1994, approximately one additional species per month was found on plots from which kangaroo rats had been removed. This difference represents only a snapshot of species diversity. Because the

Department of Biology, University of New Mexico, Albuquerque, NM 87131, USA.

*Present address: Biology Department, California State University Northridge, Northridge, CA 91330–8303, USA.

†To whom correspondence should be addressed.

total number of species each month is small, there is roughly a 60% difference in species richness between equal access and kangaroo rat removal plots. During this study, overall local diversity (total number of species observed) averaged approximately 27% higher on kangaroo rat removal plots than on equal access plots (Table 1). Compared to equal access plots, kangaroo rat removal plots supported more individuals as well as more species of other rodents. For example, during the period 1988 to 1994, an average of 117.5 individuals (of non-*Dipodomys* species) were captured on equal access plots versus an average of 231 individuals (of non-*Dipodomys* species) captured on kangaroo rat removal plots. Thus, one possible explanation of our results is that kangaroo rat removal plots contained more species simply because they contained more individuals (18). Rarefaction techniques (19, 20) take account of how the number of individuals sampled affects observed species richness and permit comparison of the number of species expected in samples of equal numbers of individuals. Application of rarefaction revealed that when 60 individuals were captured (the fewest non-*Dipodomys* individuals captured on any plot), kangaroo rat removal plots contained significantly more species (9.26) than did equal access plots (7.95 species; $P = 0.01$, Mann-Whitney U test). Thus, the increased species richness on kangaroo rat removal plots was not simply due to the greater numbers of individuals sampled.

Equal access plots typically contained one kangaroo rat species, and, after 1982, kangaroo rat removal plots contained about one more species of small granivore per month than did equal access plots (Table 1). Colonization by small granivores, therefore, was sufficient to maintain total small mammal species diversity on the experimental plots. These results contrast with recent observations on plant communities that showed that colonization by new species was not sufficient to compensate for local extinctions (21).

Our data also provide insight into the mechanisms that generated the differences in species richness. Evenness (20) was significantly lower on kangaroo rat removal plots during 1988 to 1994 [kangaroo rat removal, $J = 0.79$; equal access, $J = 0.88$ ($P = 0.01$, Mann-Whitney U test)]; more rare species were able to coexist in the absence of kangaroo rats.

The occurrence of these rare species on kangaroo rat removal plots should be attributable to some combination of higher rates of colonization and lower rates of extinction. No species showed a significantly higher colonization probability on equal access plots than on kangaroo rat removal plots during either 1982 to 1987 or 1988 to 1994 (Table 2) (22). From 1982 to 1987, only *Reithrodon-*

tomys megalotis had a significantly higher colonization probability on plots from which kangaroo rats had been excluded. From 1988 to 1994, however, five species exhibited significantly higher colonization probabilities on kangaroo rat removal plots. More important, four of the five species had similar colonization success on both old and new kangaroo rat removal plots, indicating that colonization probability for these species was related to the absence of kangaroo rats and not to the differences in vegetation structure on these plots. The remaining species, *Sigmodon fulviventer*, which is folivorous and characteristic of grassland habitats (23), exhibited a higher colonization probability on old kangaroo rat removal plots than on new kangaroo rat removal plots, indicating that its colonization was influenced by the increased grass cover on old kangaroo rat removal plots.

No species had a significantly higher extinction probability on kangaroo rat removal plots compared with equal access plots (Table 3). *Peromyscus maniculatus* had a significantly lower extinction probability on kangaroo rat removal plots from 1982 to 1987,

whereas *Perognathus flavus* and *R. megalotis* had significantly lower extinction probabilities on kangaroo rat removal plots from 1982 to 1994. From 1988 to 1994, *Peromyscus eremicus* had a significantly lower extinction probability on old kangaroo rat removal plots whereas *Chaetodipus penicillatus* had a significantly lower extinction probability only on new kangaroo rat removal plots compared with equal access plots.

Two mechanisms contributed to the higher species diversity of other rodents on kangaroo rat removal plots. The most important process was a relaxation of competitive exclusion. Six of the eight granivorous rodent species had higher colonization probabilities or lower extinction probabilities or both (Tables 2 and 3). None of the rodents exhibited the opposite pattern, which would be expected if there were strong indirect effects of competition among the rodents such that the removal of kangaroo rats would benefit a subset of small granivores, which would then competitively inhibit other species.

Kangaroo rats compete with seed-eating rodents, both by reducing their food supply

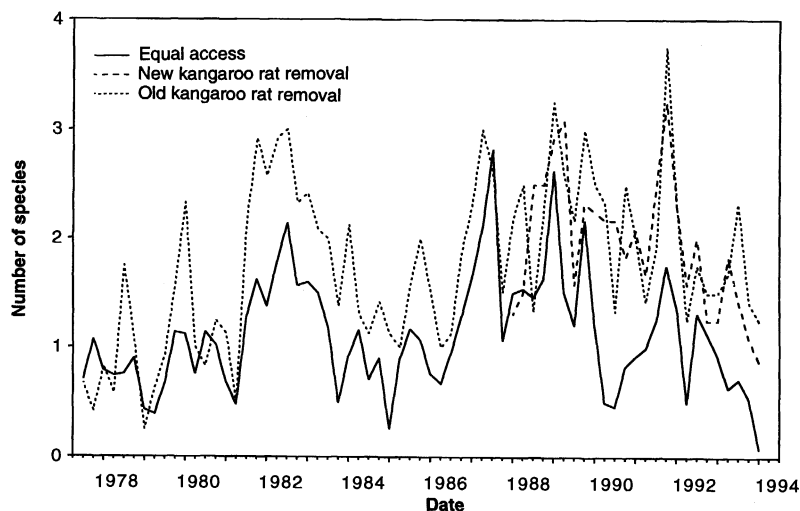


Fig. 1. Effect of different treatments on mean number of species per plot per month. Data are plotted as 3-month averages for clarity. In all analyses of data from 1988 to 1994, old versus new kangaroo rat removal plots were compared. If no significant difference was detected, the data from these plots were combined to compare kangaroo rat removal plots to equal access plots.

Table 1. Comparison of the number of non-kangaroo rat species on treatment plots by month and over years.

Treatment	1977-1981	1982-1987	1988-1994
<i>Mean number of species per plot per month</i>			
Equal access	0.83	1.28	1.20
Kangaroo rat removal	0.99	1.93*	2.09*
<i>Mean total number of species observed</i>			
Equal access	6.1	7.6	8.6
Kangaroo rat removal	8.0‡	9.3‡	11.0‡

* $P < 0.05$, equal access versus kangaroo rat removal treatment (repeated measures analysis of variance, with plots as unit of replication and months as repeated measures). † $P < 0.1$. ‡ $P < 0.05$, equal access versus kangaroo rat removal treatment (Mann-Whitney U test).

and by aggressive defense of space (13, 23, 24). Nongranivorous rodent species characteristic of desert shrub habitats (folivorous *Neotoma albigula* and insectivorous *Onychomys leucogaster* and *O. torridus*), which presumably do not compete strongly with kangaroo rats, did not respond to kangaroo rat removal (Tables 2 and 3). Whereas the responses observed largely represent habitat selection by individual rodents, all species have persisted on the plots for at least several months and been observed in reproductive condition (25).

A second mechanism, of lesser impor-

tance, was the effect of kangaroo rats on vegetation. The increase in grass cover due to the long-term removal of kangaroo rats resulted in significantly increased colonization of one species characteristic of grassland habitats (Table 2). Thus, competitive exclusion apparently accounted for six of the seven species that contributed to the higher diversity on kangaroo rat removal plots (26).

Our results show that interspecific competition affects diversity of this desert rodent community by altering metapopulation dynamics. Although early theoretical studies examined the effect of colonization

and extinction on the coexistence of competing species (27), most recent models of metapopulation dynamics have assumed that colonization and extinction are stochastic processes (8). Our results suggest that competition can have deterministic effects on probabilities of local colonization and extinction.

Experimental studies have shown that the presence or absence of a top predator can propagate through a food web, markedly altering the diversity and composition of a community (2, 28). Our results suggest that the presence or absence of a dominant competitor can have similar effects. Additions or deletions of such species change the competitive environment and alter the colonization and extinction probabilities of other species. Such cascading effects of competition have implications for conservation policies, because the extinction of native species, establishment of exotics, and reintroduction of extirpated species will often cause further changes in diversity.

Table 2. Mean colonization probabilities according to the method of Clark and Rosenzweig (22).

Species	1982-1987		1988-1994		
	Equal access	Kangaroo rat removal	Equal access	Kangaroo rat removal	
				Old	New
<i>Granivores</i>					
<i>Baiomys taylori</i>	0	0	0.004	0.063	0.011
<i>Chaetodipus penicillatus</i>	0.040	0.060	0.076	0.137	0.191
<i>C. hispidus</i>	0.003	0.012	0.006	0.004	0.004
<i>Perognathus flavus</i>	0.045	0.068	0.039	0.121*	0.129*
<i>Peromyscus eremicus</i>	0.106	0.132	0.093	0.127	0.144
<i>Peromyscus maniculatus</i>	0.059	0.220*	0.002	0.020*	0.020*
<i>Reithrodontomys fulvescens</i>	0	0.008	0.006	0.019*	0.020*
<i>R. megalotis</i>	0.094	0.311***	0.152	0.294**	0.285**
<i>Nongranivores</i>					
<i>Sigmodon fulviventor</i>	0	0	0.012	0.050*	0.008†
<i>S. hispidus</i>	0.006	0.012	0.017	0.060+	0†
<i>S. ochrognathus</i>			0.004	0.018	0.016
<i>Neotoma albigula</i>	0.193	0.159	0.096	0.063	0.071
<i>Onychomys leucogaster</i>	0.176	0.144	0.107	0.066	0.095
<i>O. torridus</i>	0.154	0.136	0.161	0.149	0.137

* $P < 0.10$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, equal access versus kangaroo rat removal treatment (t test). † $P < 0.05$ old versus new kangaroo rat removal plots (t test).

Table 3. Mean extinction probabilities (22).

Species	1982-1987		1988-1994		
	Equal access	Kangaroo rat removal	Equal access	Kangaroo rat removal	
				Old	New
<i>Granivores</i>					
<i>Baiomys taylori</i>			0.999	0.529+	0.999†
<i>Chaetodipus penicillatus</i>	0.531	0.535	0.562	0.347	0.312*
<i>C. hispidus</i>	0.999	0.393	0.620	0.500	0.250
<i>Perognathus flavus</i>	0.576	0.208***	0.686	0.348*	0.263**‡
<i>Peromyscus eremicus</i>	0.569	0.625	0.636	0.366*	0.378+
<i>Peromyscus maniculatus</i>	0.721	0.468**	0.999	0.734	0.611
<i>Reithrodontomys fulvescens</i>			0.687	0.827	0.386
<i>R. megalotis</i>	0.608	0.324**	0.548	0.230**	0.283**
<i>Nongranivores</i>					
<i>Sigmodon fulviventor</i>			0.585	0.843	0.670
<i>S. hispidus</i>	0.813	0.830	0.485	0.494	
<i>S. ochrognathus</i>			0.999	0.333	0.770
<i>Neotoma albigula</i>	0.389	0.577	0.999	0.529	0.525
<i>Onychomys leucogaster</i>	0.662	0.623	0.636	0.748	0.758
<i>O. torridus</i>	0.663	0.708	0.518	0.564	0.488

* $P < 0.1$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, equal access versus kangaroo rat removal treatment (t test). † $P < 0.1$. ‡ $P < 0.05$, old versus new kangaroo rat removal plots (t test).

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25. Maximum densities (individuals per hectare), calculated over 3-month intervals, for the most common species are as follows: *D. spectabilis*, 10.9; *D. merriami*, 17.3; *D. ordii*, 6.3; *C. penicillatus*, 5.2; *P. flavus*, 3.1; *P. eremicus*, 5.0; *P. maniculatus*, 2.5; *R. megalotis*, 7.7; *N. albigula*, 3.1; *O. leucogaster*, 2.3; *O. torridus*, 2.7. See also J. H. Brown and Z. Zeng, *Ecology* **70**, 1507 (1989).
26. A third possible mechanism, a difference in predation between kangaroo rat removal and equal access plots, does not appear to be important. All avian and mammalian predators had equivalent access to both types of plot. The only predators differentially affected by our manipulations were large-bodied snakes, which were unable to pass through the small gates on kangaroo rat removal plots. If such snakes had a significant effect, however, we would have expected

- differences in colonization or extinction probabilities of *Onychomys* spp. and *N. albigula*, which should be as susceptible to snake predation as granivorous rodents (Tables 2 and 3) [see also (13)].
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Synergistic Roles for Receptor Occupancy and Aggregation in Integrin Transmembrane Function

Shingo Miyamoto, Steven K. Akiyama, Kenneth M. Yamada*

Integrin receptors mediate cell adhesion, signal transduction, and cytoskeletal organization. How a single transmembrane receptor can fulfill multiple functions was clarified by comparing roles of receptor occupancy and aggregation. Integrin occupancy by monovalent ligand induced receptor redistribution, but minimal tyrosine phosphorylation signaling or cytoskeletal protein redistribution. Aggregation of integrins by noninhibitory monoclonal antibodies on beads induced intracellular accumulations of pp125^{FAK} and tensin, as well as phosphorylation, but no accumulation of other cytoskeletal proteins such as talin. Combining antibody-mediated clustering with monovalent ligand occupancy induced accumulation of seven cytoskeletal proteins, including α -actinin, talin, and F-actin, thereby mimicking multivalent interactions with fibronectin or polyvalent peptides. Integrins therefore mediate a complex repertoire of functions through the distinct effects of receptor aggregation, receptor occupancy, or both together.

Transmembrane integrin receptors for extracellular matrix proteins mediate signal transduction, but they also participate in organizing cell adhesion sites and the actin-containing cytoskeleton (1). How a single receptor can fulfill these multiple functions, as well as show selectivity in effects on specific cytoskeletal proteins, was examined by comparing the relative roles of receptor occupancy and aggregation. We hypothesized that even though simple aggregation of a number of cytokine and hormone receptors can mediate normal transmembrane signal transduction in place of ligand occupancy (2), some receptors might be able to assign distinct functions to three types of transmembrane signal: ligand occupancy, receptor aggregation, or both together. We determined the requirements for integrin-mediated transmembrane control of the localization of specific cytoskeletal proteins and for transmembrane signaling involving tyrosine phosphorylation. We found that (i) integrin receptors induce

distinct cellular responses to binding of a ligand, to aggregation, or to a combination of the two; (ii) integrin receptors can control the distribution of specific cytoskeletal proteins (one protein was controlled by simple receptor aggregation, whereas six other cytoskeletal proteins required a combination of both aggregation and ligand binding); and (iii) the most proximal molecular interactions with integrin cytoplasmic domains appear to involve the cytoskeletal protein tensin and the tyrosine kinase pp125^{FAK} (focal adhesion kinase), rather than the previous candidates talin and α -actinin.

Polystyrene beads coated with substrates and antibodies served as mediators of integrin occupancy or aggregation, whereas soluble monovalent ligands provided simple ligand occupancy. Beads coated with fibronectin mimic adhesive site generation (3) and can induce transmembrane aggregation of a variety of cytoskeletal molecules including F-actin (Fig. 1, A and B). We developed procedures to quantitate this process and detected similar bead-induced transmembrane aggregation with talin, α -actinin, tensin, vinculin, paxillin, and filamin (Fig. 2A) (4, 5). In addition, pp125^{FAK} also showed bead-induced clus-

tering, whereas tubulin did not (Figs. 1C and 2A). Similar results were obtained with beads coated with multivalent Arg-Gly-Asp (RGD)-containing peptide conjugates (Fig. 2A) and with adhesion-blocking monoclonal antibodies (mAbs) to either the α_5 or β_1 subunit of the fibronectin receptor (Fig. 1, G to I, and Fig. 2B). These multivalent antibody ligands induced transmembrane aggregation of all seven cytoskeletal proteins and FAK, but not tubulin, lactate dehydrogenase, or Jak-2 (Fig. 1C) (6). Little or no clustering of any cytoskeletal protein or FAK was observed with beads coated with polylysine or concanavalin A (Fig. 1, D to F, and Fig. 2A).

Unexpectedly, mAbs that do not inhibit cell adhesion displayed a distinct and specific subset of these properties. The mAbs 11, to the α_5 subunit, and K20, to the β_1 subunit, do not inhibit cell adhesion (6–9) and will hereafter be termed noninhibitory antibodies. Each of these noninhibitory mAbs coated on beads effectively induced transmembrane aggregation of tensin in patterns that were indistinguishable from tensin aggregation induced by adhesion-blocking mAbs and multivalent ligands (Figs. 1K and 2B). However, no significant coclustering of F-actin, talin, α -actinin, vinculin, paxillin, or filamin could be detected (Figs. 1J and 2B). Interestingly, FAK was also readily coclustered by these noninhibitory mAbs (Figs. 1L and 2B). Three other mAbs to the β_1 subunit were compared and had similar patterns; for example, noninhibitory mAbs DF5 and LM534 induced aggregation of FAK but not F-actin, whereas adhesion-blocking mAb P4C10 induced aggregation of both FAK and F-actin (6).

It is now well established that ligand- or antibody-induced clustering of a number of growth factor, hormone, and other receptors can mediate transmembrane signal transduction, including integrin-mediated tyrosine phosphorylation of FAK (2, 10). As expected if simple aggregation alone triggers integrin signaling, beads coated with noninhibitory mAbs that do not bind to an active site stimulated tyrosine phosphorylation that could be detected by anti-

Laboratory of Developmental Biology, National Institute of Dental Research, National Institutes of Health, Bethesda, MD 20892–4370, USA.

*To whom correspondence should be addressed.