

while not inconsistent with stochastic accretion, are unexpected in this process (32) and may suggest that their obliquities have evolved since formation. (iii) We have assumed that each impactor is completely accreted when it strikes a planet; in large impacts, particularly at high velocities, fragmentation and loss of ejecta with high angular momentum may be important (34). (iv) The spin rates of Jupiter and Saturn, which probably arose during the accretion of their gas envelopes, are not understood theoretically and merit detailed hydrodynamic calculations. In contrast, our results may apply to Uranus and Neptune, ~90% of whose mass consists of solids. Applying Eq. 13 implies $m_1/M_p \approx 0.15$, similar to the values deduced for the terrestrial planets. The large obliquities of Uranus (98°) and Neptune (29°) are also consistent with stochastic accretion, although the obliquities of the giant planets may alternatively have arisen from rotation of the ecliptic plane after planet formation was complete (7).

Note added in proof: A new preprint by Laskar and Robutel (35) argues that the obliquity of Mars wanders chaotically over the range 0° to 60° and that the obliquities of all the terrestrial planets may have passed through chaotic states in the past. Their results strengthen the case for stochastic accretion by implying that the primordial obliquity of Mars may have been as large as 60°; however, chaotic obliquity evolution provides a possible mechanism for reversing the spin of Venus, so the primordial spin of Venus may have been prograde. Chaotic obliquity evolution does not affect arguments for stochastic accretion based on spin rates because it changes only the orientation, not the magnitude, of the spin vector.

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Mechanisms in the Competitive Success of an Invading Sexual Gecko over an Asexual Native

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The competitive displacement by a sexual gecko species of an asexual resident gecko has been documented over a wide geographic area. To test hypotheses concerning the detailed mechanism of this displacement, an experimental system was developed to follow populations of geckos in a duplicated, controlled environment that closely approximates the natural arena for the competitive interaction. Asymmetric competition occurred only in the presence of light, which attracts a dense concentration of insect food sources. The mechanism of competition was partly due to the behavioral dominance of the larger sexual species over the smaller asexual species in areas near the concentrated food. However, this behavior resulted from an avoidance response of subordinate asexuals rather than overt aggression by the sexual species.

The mechanisms that enable exotic species to thrive at the expense of native species are often unclear. There are many examples of the decline of native species after the arrival of an exotic species (1, 2). A competitive mechanism is frequently proposed to explain such phenomena, but rarely has such a mechanism been isolated and tested in an experimental setting, especially in vertebrates.

We have documented the recurrent human-aided arrival and distribution of the house gecko *Hemidactylus frenatus* to islands in the tropical Pacific Ocean and the concomitant numerical decline of species that previously occupied buildings on these islands (3). The invader *H. frenatus* is a sexual species, whereas at least two of the species it supplants are asexual partheno-

gens, *Hemidactylus garnotti* and *Lepidodactylus lugubris*. Around the time of World War II *H. frenatus* reached Oahu, Hawaii, and reached Fiji, Vanuatu, and Samoa probably in the last 20 years (2). It was first recorded in Tahiti in 1988 and on the Micronesian islands of Arno Atoll, Ponopei, and Kosrai this year (specimens are in the California Academy of Science).

Documentation of the decline of gecko species that previously occupied the nocturnal, insectivorous house gecko niche comes from two sources: a comparison of historical collection records to current census surveys (3) and a 5-year experiment in Suva, Fiji (4). On islands like the Cook Islands that have yet to be colonized by *H. frenatus*, *L. lugubris* is extremely common on buildings, whereas *H. garnotti* is patchy in distribution and abundance. These studies present unambiguous evidence of the strong dominance of *H. frenatus* over *L. lugubris*. How-

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ever, they do not illuminate the mechanism by which *H. frenatus* overcomes a twofold disadvantage when compared to *L. lugubris* in reproductive success (5) to emerge as the most abundant gecko species in the urban-suburban landscape. In laboratory enclosures, *H. frenatus* is behaviorally dominant to *L. lugubris* (6) for two reasons: adult *H. frenatus* are larger in body length and mass than *L. lugubris* [in these species and other lizards, body size and dominance are correlated (7)] and in size-matched individuals, males, which appear only in *H. frenatus*, are more aggressive than asexual females.

Field counts of the two species in different habitats reveal that the competitive exclusion is primarily confined to urban and suburban habitats (particularly in the more xeric parts of islands), whereas in native villages or native forest habitats the most common gecko is often *L. lugubris* (3, 8). These observations suggest that the urban environment augments the competitive advantage of *H. frenatus*.

To account for these observations, we hypothesized that the agonistic dominance of *H. frenatus* over *L. lugubris* would lead to competitive success when insect prey were concentrated in areas that could be defended by the larger and more aggressive *H. frenatus*. Buildings with lights act like giant insect malaise traps because lights attract high concentrations of insects, the building's vertical walls intercept their flight paths, and the upward movements of the insects are further impeded by overhanging eaves.

Figure 1 summarizes the biogeographic pattern of displacement of *L. lugubris* by *H. frenatus* by comparison of the densities in sympatry and allopatry (2) and on electrically lighted (dotted lines) and unlighted (solid lines) buildings are shown (*Cp* = *Cosymbotus platyurus*). Density is the logarithm of the number of geckos seen, per investigator, per minute of search time during a slow walk around buildings with headlamps. This measure of density is highly correlated with actual density estimates based on multiple mark-and-recapture studies ($r = 0.81$; $P = 0.0007$). P values [from two-factor analyses of variance (ANOVAs)] that contrast geographic areas are 0.228 for *H. frenatus* and 0.0001 for *L. lugubris*, and P values that contrast lighted and unlighted buildings are 0.36 for *H. frenatus* and 0.70 for *L. lugubris*. Numbers of *L. lugubris* drop precipitously on islands that *H. frenatus* has invaded (region *Hf* + *LI*). The overall abundance of geckos on buildings declines in areas in which *L. lugubris* increases in abundance (mid- and eastern Pacific).

densities on lighted versus unlighted buildings (Fig. 1), which supports our hypothesis that light may influence the observed patterns. Because insect densities are high near the lights and the flat structure of building walls makes these concentrated resources defensible (10), we hypothesized that behavioral exclusion by *H. frenatus* of *L. lugubris* in these areas would be a more likely mechanism of competition than resource depletion.

We investigated the role of light in this competitive displacement at the scale of the population as well as at the scale of the individual. First we tested two alternative hypotheses: (i) Competition does not occur between these species and (ii) competition occurs and is affected by the insect aggregation around lights. We subsequently tested our hypothesis that the mechanism involves the exclusion of *L. lugubris* by *H. frenatus* from the concentrated insect resource around the light.

Our experimental units were 18 replicate aircraft hangars (11) at Barbers Point Naval Air Station on Oahu, Hawaii (Fig. 2). These units are structurally similar to houses and nearly as large, thus mimicking the natural setting in which the competitive displacement occurs. Each hangar received a total of 20 geckos (12). We used a nested two-factor experimental design: *H. frenatus* alone, *L. lugubris* alone, and *H. frenatus* and *L. lugubris* combined, each with and without light. Each of the six experimental paradigms was run in parallel in three hangars (18 total). All experimental populations were taken from lighted urban environments in which both species were present. For the experiments with two species, an equal number (ten) of each species was used, whereas 20 of each were used in the single-species treatments. Each *H. frenatus* group was stocked at an equal sex ratio. In lighted treatments, a small fluorescent light (8 W) was placed at the back and center of the hangar (13). The

relative positions of the lighted and unlighted hangars are shown in Fig. 2.

Censuses (13 in all) were conducted every 8 days and consisted of measurements of each gecko's weight, snout-vent length, egg production (visible through the semi-transparent ventral abdominal skin), and tail length (14). Insect abundances were also counted at 8-day intervals (15). Relative body condition at each census was assessed by each gecko's residual deviation from a linear regression of the log of body weight versus snout-vent length (16). Dead and missing geckos were replaced at tri-weekly restockings. Occasionally, missing geckos (those that were absent in two consecutive censuses) would reappear after restocking; gecko numbers per hangar were maintained between 15 and 21. Survivorship was estimated as the proportion of introduced geckos remaining after a given time interval. Fecundity was measured as the sum of the number of state changes per egg for each species in a given hangar (17).

Night foraging position near the light was assessed with additional observational units that were constructed to help monitor behavioral interactions of geckos foraging

Fig. 1. Gecko density with regard to geographic location and light. The mean densities (and standard errors) of *H. frenatus* (*Hf*) (top two plots) and *L. lugubris* (*LI*) (bottom two plots) in sympatry and in allopatry (2) and on electrically lighted (dotted lines) and unlighted (solid lines) buildings are shown (*Cp* = *Cosymbotus platyurus*). Density is the logarithm of the number of geckos seen, per investigator, per minute of search time during a slow walk around buildings with headlamps. This measure of density is highly correlated with actual density estimates based on multiple mark-and-recapture studies ($r = 0.81$; $P = 0.0007$). P values [from two-factor analyses of variance (ANOVAs)] that contrast geographic areas are 0.228 for *H. frenatus* and 0.0001 for *L. lugubris*, and P values that contrast lighted and unlighted buildings are 0.36 for *H. frenatus* and 0.70 for *L. lugubris*. Numbers of *L. lugubris* drop precipitously on islands that *H. frenatus* has invaded (region *Hf* + *LI*). The overall abundance of geckos on buildings declines in areas in which *L. lugubris* increases in abundance (mid- and eastern Pacific).

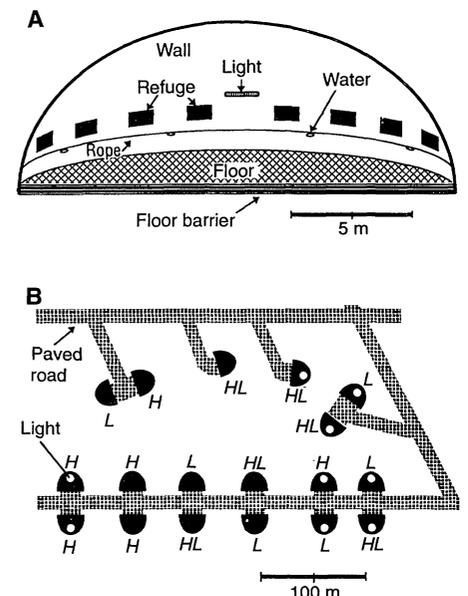
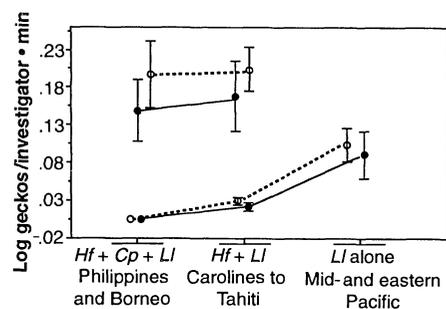


Fig. 2. Experimental units. Each of the 18 aircraft hangars was modified for experimental purposes. (A) Teflon paint (Fluon) was painted around the entire entrance and on the floor barrier to keep geckos from leaving or entering. Eight refuges (dark rectangles) were mounted on the wall and used by geckos during the day. The entrance is approximately 17 m across by 5 m high, allowing free passage of natural insects. (B) Orientation of the various hangars (dark half circles) relative to each other. Species combinations are noted in capital letters (*H* = *H. frenatus*, *L* = *L. lugubris*). Hangars with lights (shown with a white dot) faced each other so that lights were never visible to geckos or insects in the dark treatments.

near a light (18). All intraspecific and interspecific pairwise encounters were recorded and scored in the manner of Bolger and Case (6).

To confirm that insects were aggregating as expected in our experimental units, we plotted the density of insects against distance from the center of the hangar (the location of the lights in lighted treatments) (Fig. 3). There were significantly more insects in the lighted hangars overall, and in these hangars there were significantly more insects near the light.

Figure 4 shows the relative condition of *L. lugubris* and *H. frenatus*, respectively, for the last six census intervals. The majority of individuals were either from the initial introduction or from a major restocking at interval six. Each trajectory follows the mean of three replicate hangars. Light for both species and the interaction of competitor and light for *L. lugubris* were the only statistically significant factors in these comparisons. They were significant even if only core individuals (from initial stocking) were considered.

The two-factor fecundity analysis did show a significant effect for light ($P < 0.01$ for *H. frenatus* and *L. lugubris*) but no strong trend for competitor or interaction effects ($P > 0.16$ for *L. lugubris* and $P > 0.4$ for *H. frenatus*) in the lighted treatments. Means for both species in the lighted treatments ranged from 1.7 to 2.2 and in the dark they ranged from 0.5 to 0.9.

Survivorship was calculated as the proportion that lived from initial introduction to at least the end of the experiment. Lighted treatments had higher survivorship ($P < 0.02$ for both species), but the presence of a competitor or interaction of light and competitor had no effect ($P > 0.4$ for both species). Mean survivorship in the light was typically between 30 and 50%, and in the dark it ranged from 12 to 18%.

Analysis of the pairwise interactions observed in the small behavioral enclosures indicated high levels of agonism (19). When alone, *L. lugubris* formed a stable dominance hierarchy, with dominant (alpha) individuals occupying positions closest to the light and subordinate (nonalpha) individuals kept away from the light. The *H. frenatus* geckos showed a similar pattern when alone. However, alpha males kept other males off of the 5-m² wall entirely, whereas females (in the small numbers stocked) showed no aggression toward other females.

Figure 5 shows the effect of *H. frenatus* on the position of *L. lugubris* in relation to light. Subordinate *L. lugubris* were significantly less aggregated toward the light in the presence of *H. frenatus*. Dominant *L. lugubris* were unaffected by the presence of *H. frenatus* and were actually found closer

to the light. Thus, the interaction term of dominance and competitor is significant. However, *H. frenatus* did not show direct aggression toward any *L. lugubris*. The subordinate *L. lugubris* moved farther from the light to avoid the *H. frenatus* that had congregated there to forage (Fig. 4). Our

results suggest that the competitive mechanism that affects condition occurs only in the light (with highly concentrated insect distributions) and is asymmetric. This finding is consistent with the observed regional displacement patterns of *L. lugubris* by *H. frenatus* as well as with the hypothesis that

Fig. 3. Insect density in relation to light. Insect density (\pm SEM) was calculated as the number of insects per trap per census interval, weighted by gecko preference and averaged within treatments. The insect survey spanned seven census intervals (8 days per interval). Insect density in lighted units (solid lines) was significantly higher than in darker units (dashed lines) overall (two-factor ANOVA, $P < 0.001$), and the interaction of light and distance from light was also significant ($P < 0.001$). It was impractical to maintain traps closer to the light for the duration of the study.

We estimated insect density at a distance of 0.1 m from the light by averaging the density obtained in a single night sample of four traps. When this value was projected to span a complete census interval (for comparison with the other values in the figure), the calculated density was well over 1000. This value represents a more than 33-fold increase in insect density between measurements taken from 2.5 m and from 0.1 m, respectively.

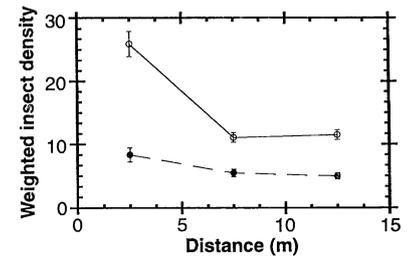


Fig. 4. Effect of competitor on relative condition. Mean relative body condition is plotted for the last six census intervals. Relative condition is the residual deviation from the regression of the logarithm of weight versus snout-vent length for all geckos of the same species for each census interval. Each point represents the mean of three replicates of the treatment. A two-factor ANOVA was used for each species for each census interval, with units (hangars) as an additional nested random factor. (A) For *L. lugubris*, the effect of light is statistically significant for censuses 8, 9, 11, and 12 (all $P < 0.02$). The P values for the interaction effects of light and competitor for the last three censuses are 0.05, 0.01, and 0.06, respectively. In lighted treatments, the effect of *H. frenatus* is statistically significant for the last three censuses (one factor, nested ANOVA, $P = 0.03$, 0.002, and 0.03, respectively). If only core individuals from the initial introduction are considered, the interaction terms for the last three censuses are all significant at $P < 0.02$. (B) For *H. frenatus*, light is statistically significant for all six censuses ($P < 0.02$ for all), and none of the interaction terms is significant ($P > 0.3$). The nested factor (hangar) is significant only in census 10 with respect to *L. lugubris* ($P < 0.01$). These results demonstrate the asymmetric competitive effect of *H. frenatus* on *L. lugubris* and that it occurs only in the light.

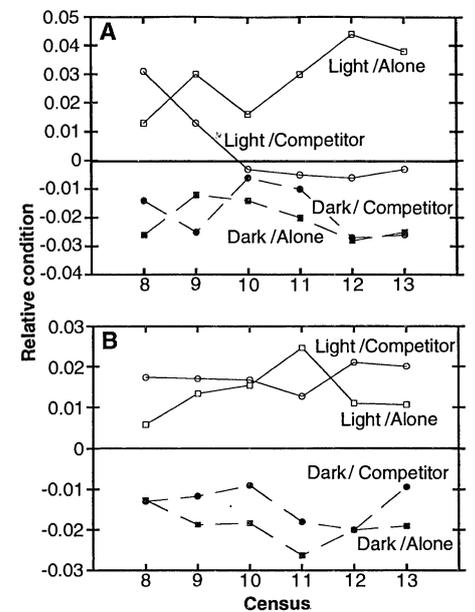
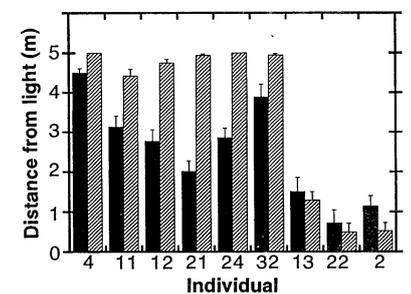


Fig. 5. Effect of *H. frenatus* on *L. lugubris* position. Positions of individual *L. lugubris* (shown by identification numbers) in relation to light in small behavioral observation units were recorded before (solid bars) and after (shaded bars) the addition of *H. frenatus*. Distances are according to regions (error bars, SEM). Observations are 15-min time point positions taken over 14 days from 1900 to 2200 hours. We used an ANOVA with two factors: before and after *H. frenatus* and dominant and subordinate (alpha and nonalpha). This analysis reveals a significant effect for dominance (individuals 22 and 2) ($P < 0.02$), presence of *H. frenatus* ($P < 0.001$), and the interaction of dominance and *H. frenatus* presence ($P < 0.0001$). Repeated within individuals, these P values are 0.001, 0.7, and 0.05, respectively. The species *H. frenatus* significantly excludes subordinate *L. lugubris* from the dense insect concentration around the light.



depicts light as a key factor mediating this displacement.

One important mechanism of the success of *H. frenatus* is a form of behavioral dominance, which asserts itself most effectively only when food resources are aggregated in a structurally simple environment. Our design enabled geckos to see other geckos on the wall 360° around the light. Subordinate *L. lugubris* were displaced from the light after the addition of *H. frenatus* and presumably experienced fewer foraging opportunities. Lighted hangars have not only higher concentrations of food but greater amounts of food overall compared to dark hangars (Fig. 3). Thus, decline in body condition of *L. lugubris* in lighted hangars in the presence of *H. frenatus* is all the more convincing.

This behavioral dominance did not result from directed action of *H. frenatus* toward *L. lugubris*. Instead, *L. lugubris* avoided *H. frenatus*, retreating as the competitor foraged near the light. A related interference mechanism that was not tested here also could be operating. The foraging efficiency of *L. lugubris* would be further reduced if it were less likely to chase insects or more likely to abandon chases in the presence of *H. frenatus*.

We have not ruled out the potential contribution of other mechanisms. When food resources are concentrated, *H. frenatus* may be more efficient at capturing insects and so deplete the population available to *L. lugubris*. Indeed, *H. frenatus* appear to move faster and farther to capture insects than *L. lugubris*. Such a mechanism of exploitative competition need not be mutually exclusive of the observed behavioral interference. Both of these and other mechanisms could be involved, but we do not yet know the relative contribution of each.

For cross-generational numerical effects to occur, survivorship, fecundity, or both must be affected by the presence of the competitor. In previous studies of these same species, body condition has been shown to correlate with future changes in fecundity and survivorship (4). Our investigation of these two traits did not show the strong interaction effect seen with relative body condition. This lack of direct correlation is primarily due to two design factors: (i) The competitive effect is manifested initially on body condition, which later translates into reductions in survivorship and in fecundity. The time lag for these effects could be beyond the duration of the study. (ii) Our initial expectations that strong intraspecific interactions would not occur in *L. lugubris* (6) were contradicted by behavioral observations (19). In our experimental design, all hangars were stocked with 20 individuals. Thus, when *L. lugubris* was in the presence of *H. frenatus*, its

intraspecific density was reduced by half (from 20 to only 10 *L. lugubris* plus 10 *H. frenatus*). Consequently, our design was a conservative one for detecting interspecific competition because we simultaneously reduced intraspecific competition in two-species treatments.

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11. Each hangar is a concrete half-dome similar in size and shape to a concert shell (17 m wide by 14 m deep by 6 m high) with an asphalt floor. Insects can fly freely in and out of the large open end. Cracks that would have provided gecko hiding places were plugged with spray-foam insulation. Before the start of the experiment, all geckos naturally occupying the hangars were removed. The most common species found in the hangars was *H. frenatus*. The relative abundance of native species at the site was 85% *H. frenatus*, 9% *G. mutilata*, 6% *L. lugubris*, and <1% *H. typus*. We enhanced the gecko suitability of the bunkers in several ways. A rope 2 cm in diameter was strung along the entire circumference of each hangar at a height of 1.3 m to provide a horizontal surface for gecko movements and to provide hiding areas. Eight specially constructed refuges provided daytime hiding places for geckos and facilitated our census-taking. Each two-layered refuge (30 cm by 25 cm) was mounted on the wall at a height of 2 m. The layer closest to the wall was made of transparent Plexiglas and was mounted with unequal spacing to provide between 0.5 and 1.5 cm of depth between it and the wall. This material allowed for thigmotactic stimuli for the range of gecko body size used in the experiment. A second layer of black carpet was then attached to the first Plexiglas layer with Velcro. To take censuses, we folded up the carpet and viewed the geckos through the Plexiglas. A small wire was used to prod them from the refuge. Geckos had free access to water throughout the experiment. They were confined within hangars by the use of Fluon AD-1 (Northern Products, Woonsocket, RI), a Teflon-based paint on which geckos cannot walk. Two Fluon stripes were painted (12 cm wide, two coats) on the walls and ceiling near the open end of the hangars. One was designed to keep experimental geckos in, the other to keep local geckos out. An aluminum barrier 20 cm high was nailed to the asphalt floor and also coated with Fluon. In the enclosure, an additional stripe of Fluon was painted approximately 10 feet high to facilitate census-taking. Mammalian predators (feral cats and mongooses) are common on the site and were excluded by fences placed in front of each hangar. The abundance and spatial distribution of insects in the hangars were monitored with six insect sticky traps (24 cm by 12 cm, ABEPSCO, Orange, CA) per hangar. Each was suspended at a height of 2 m and a distance from the wall surface of 35 cm with a wire coated with plastic and Fluon to keep geckos away from the traps. Because the area was patrolled regularly by security guards, human interference was kept to a minimum. The full experiment ran from November 1991 to March 1992.
12. To stock the experiments, we collected adult geckos from necessarily different areas where we could obtain large numbers of the two species. We collected *H. frenatus* at Wailua on the north shore of Oahu, whereas most *L. lugubris* were collected from Kaneohe on the windward (eastern) side of Oahu and from Hilo on the windward side of Hawaii. Geckos about to lay eggs or appearing unhealthy were excluded. A subsample of each species ($n = 20$) was examined for blood and gut parasites. We found no blood parasites after examining Giemsa-stained blood smears. A few individuals of both species had coccidia in fecal samples and cestodes or nematodes in their guts (K. Hanley, unpublished data). We marked the geckos by clipping the tips of their toes in an identifiable pattern (2) and by painting recognizable patterns on their backs with water-based paint.
13. The 8-W fluorescent lights were controlled by a system of 12-V deep-cycle batteries and photo-sensitive switches that automatically turned the lights on at dusk and off at dawn. Batteries were recharged approximately every 8 days. No other electric lights were present within a perimeter of at least 1 km.
14. Gecko weight was measured to the nearest 0.1 g, and snout-vent length was measured to the nearest 0.5 mm. Eggs were counted and scored as none (<5 mm), medium (5 to 8 mm), or large (>8 mm). Tail condition was judged by the proportion of tail present (by weight). All individuals with <50% of their tails remaining were removed from the analyses. All measurements were taken by the same investigator (K.P.) throughout the study.
15. Insects were scored according to body length, taxon, and activity period. Each of these categories was given a crude weight index that reflected its qualitative rank (0 to 4) in gecko diets (2). Large wasps that are never eaten, exclusively day-flying insects, and arthropod taxa that geckos avoid (such as centipedes and scorpions) were given a rank of 0. Termite alates received the highest rank of 4. For each trap, we multiplied the number of insects by these weights and then summed them to arrive at the weighted insect abundance. All statistics included these summed weighted measures, although the same trends and conclusions were produced by unweighted sums.
16. The regression for the condition index included all geckos of the same species for a given census interval. Measures of condition, weight, or both that rely on values from the beginning of the experiment reflect the collection environment and thus are inappropriate for comparative analyses. For organisms belonging to the same generation, measures of demographic success (such as condition) are highly correlated with numerical changes in abundance in our 5-year study of the same gecko species in Fiji (4) and with measures of other lizard taxa [A. E. Dunham, *Ecol. Monogr.* **50**, 309 (1980)].
17. A state change is growth between census inter-

vals from no egg to small egg or an increase in egg size from small to medium or medium to large. A change from large to no egg was interpreted as a successful laying event and given an equivalent score. Total egg state changes were divided by the number of females in the unit to yield a per capita fecundity index. This index was used instead of the number of eggs laid per female because a number of females began and finished the experiment with partially developed eggs.

18. In a 19th hangar, four small sections of wall (1.75 m by 2.5 m) were isolated with Fluon and aluminum floor barriers. Each unit was equipped with four small (20 cm by 15 cm) refuges. Two refuges were positioned 1.5 m off the floor and two were 0.75 m high, with one water dish centered in the middle of the four. Each unit contained one light mounted on the wall 2.1 m high. The region around the light was narrowed to about 1 m² with strips of Fluon. The position of all four units together made observation from one large blind possible, with the observer 2 m from the light. Eight geckos were placed in each unit, and two units could be watched simultaneously. Geckos were marked and painted as described in (12). Positions of all individuals were noted at 15-min

intervals and scored as follows: 0 = on light, 1 = within 20 cm above or below, 2 = within 20 cm on the sides in the shadows, 3 = 20 to 50 cm, 4 = 50 cm to 1.2 m, and 5 = > 1.2 m or not visible. These marks were measured and drawn on the walls around the light to facilitate accuracy. During the initial phase, species were isolated (units A and B with *L. lugubris* and units C and D with *H. frenatus*) and geckos were allowed to acclimatize to the light and surroundings. After 20 days, including 9 days of data gathering, the four least phototoxic *L. lugubris* in A and B were replaced with the four most phototoxic *H. frenatus* from C and D, respectively (two males, two females). The *H. frenatus* immediately adjusted and moved toward the light in their new enclosures. Positions were again scored at 15-min intervals for 6 days after the switch. During these observations (which spanned the month of March) lights were only turned on when data were being recorded (daily from 1900 to 2200).

19. Alpha individuals were defined as those that never retreated from an encounter with another individual of the same species in the enclosure, and all encounters culminated with the retreat of one of the participants. Before species were com-

bined, there were two alpha individuals for each species (two enclosures each). After the species were combined there were four alphas of each species (four enclosures), with only two focal enclosures reported here. Intraspecific and interspecific interactions were recorded in the combined treatments. The frequencies of the pairwise interactions were: *L. lugubris*-*L. lugubris*, 160 in 30 hours of observation (5.4 per hour); *H. frenatus*-*H. frenatus*, 25 in 16 hours (1.6 per hour); and *H. frenatus*-*L. lugubris*, 39 in 12 hours (3.25 per hour). In approximately half of the *H. frenatus*-*L. lugubris* interactions, a dominant *L. lugubris* attacked an *H. frenatus*, and in the other half, a subordinate *L. lugubris* retreated from a nonaggressive *H. frenatus*. The approaches of *H. frenatus* were termed nonaggressive when they continued on the same path unaffected by the retreating *L. lugubris*.

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Two Open Complexes and a Requirement for Mg²⁺ to Open the λP_R Transcription Start Site

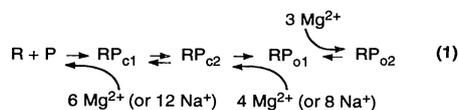
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Potassium permanganate (KMnO₄) footprinting in the absence and presence of magnesium (Mg²⁺) at the λP_R promoter identified two different open complexes with *Escherichia coli* Eσ⁷⁰ RNA polymerase (designated RP_{o1} and RP_{o2}). The single-stranded region in RP_{o1} (formed in the absence of Mg²⁺) was at most 12 bases long, whereas that in RP_{o2} (formed in the presence of Mg²⁺) spanned at least 14 bases. Only in RP_{o2} did the single-stranded region extend to the start point of transcription (+1, +2). These results provide a structural basis for the requirement for uptake of Mg²⁺ in the formation of RP_{o2} from RP_{o1}, as deduced from kinetic studies at this promoter.

The formation of an open complex between RNA polymerase (RNAP) and promoter DNA involves passage through a series of intermediate complexes that involve conformational changes in both RNAP and DNA (1, 2). Kinetic-mechanistic (3) and structural (4-6) characterizations demonstrated that RNAP (R) and promoter (P) form an initial specific closed complex at the promoter (RP_{c1}), an intermediate closed complex (RP_{c2}) that involves a major conformational change in RNAP, and an open complex (RP_o) in which the DNA in the vicinity of the start site is single-stranded. No studies to date have probed the steps of the process of DNA strand opening. It is unknown if opening is a sequential or an all-or-nothing process and if sequential, which regions are opened early and which are opened late.

Chemical probing of RNAP-λP_R open complexes with KMnO₄ in the presence and absence of Mg²⁺ provides some answers to these questions.

On the basis of the effects of MgCl₂ on the dissociation rate constant of open complexes at the λP_R promoter in the absence of initiating nucleotides, we (1) deduced that Mg²⁺ is required for the formation of an initiation-competent open complex designated RP_{o2} to distinguish it from the open complex that exists in the absence of Mg²⁺ (RP_{o1}). We proposed (1) a mechanism (Eq. 1) in which Mg²⁺ has a specific stoichiometric role in the isomerization of RP_{o1} to RP_{o2}:



According to this mechanism, RP_{o1} is converted to RP_{o2} upon uptake of approximately three Mg²⁺ cations, presumably at specific sites on RNAP. In contrast, Na⁺ or Mg²⁺ (or other cations, if present) function nonspecifically as cation competitors for RP_{c1} and RP_{o1}.

KMnO₄ preferentially oxidizes unpaired or distorted pyrimidines in DNA (T >> C) (7) and has been used to detect single-stranded regions of DNA in RNAP-DNA complexes (8-10). To characterize the two open complexes at the λP_R promoter deduced from kinetic studies, we probed the accessibility of pyrimidines in these complexes to oxidation by KMnO₄ in the presence and absence of Mg²⁺. The KMnO₄ reactivity of the top and bottom strands is shown in Fig. 1, A and B, respectively, and summarized in Fig. 1C. Radioanalytic imaging (11) provides a quantitative comparison of the reactivities of pyrimidines to KMnO₄ in the presence and absence of Mg²⁺ (Fig. 1D).

RNAP formed open complexes on supercoiled plasmid DNA at the λP_R promoter from 4° to 37°C both in the presence and in the absence of 10 mM Mg²⁺ (Fig. 1). However, Mg²⁺ enhanced KMnO₄ modification at many positions, especially at both boundaries of the open region where the ratio of KMnO₄ reactivity in the presence of Mg²⁺ to that in the absence of Mg²⁺ was in the range of 3 to 8 (Fig. 1D). Positions +1T and +2T, unreactive or weakly reactive with KMnO₄ in the absence of Mg²⁺, became accessible to reaction with KMnO₄ in the Mg²⁺-induced open complex. In a similar manner, a large enhancement of KMnO₄ reactivity of -11T and -12C was observed in the presence of Mg²⁺. In contrast, enhancement was more modest in the central part of the open region (positions -3T, -4T, -8T, -9T, and -10T) where the ratio of KMnO₄ reactivity in the presence of Mg²⁺ to that in the absence of Mg²⁺ was ≤ 3 (12).

Together, these data indicate a significant difference in the open complex in the presence and absence of Mg²⁺. In the absence of Mg²⁺, the extent of strand

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