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 asexualls 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 into 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 displants are asexual partenogens, 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 Aroll, Ponopei, and Kosrae 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 encounters, *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 sympathy and allopatry. This displacement results in a numerical decline in *L. lugubris* rather than a proportional increase in *H. frenatus* relative to *L. lugubris*. Lighted buildings support significantly higher numbers of gekkos than do dark buildings (9), which suggests that insects may be a limiting resource. Both species maintain higher 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 gekkos (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 gekkos were replaced at triweekly restockings. Occasionally, missing gekkos (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 gekkos 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 gekkos foraging

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**Fig. 1.** Gecko density with regard to geographic location and light. The mean densities (and standard errors) of *H. frenatus* (*H*) (top two plots) and *L. lugubris* (*L*) (bottom two plots) in sympathy and in allopatry (2) and on electrically lighted (dotted lines) and unlighted (solid lines) buildings are shown (CB = Cosymbotus platyurus). Density is the logarithm of the number of gekkos 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 *H* + *L*). The overall abundance of gekkos 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 gekkos from leaving or entering. Eight refuges (dark rectangles) were mounted on the wall and used by gekkos 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 gekkos 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 (±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 dark 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 (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.](image1)

![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.](image2)

![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.](image3)
departs light as a key factor mediating this displacement.

One important mechanism of the suc-
cess of H. frenatus is a form of behavioral
dominance, which asserts itself most effec-
tively only when food resources are aggre-
gated 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 re-
sult from directed action of H. frenatus
with L. lugubris. Instead, L. lugubris
avoided H. frenatus, retreating as the com-
petitor 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 mecha-
nisms 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 inves-
tigation of these two traits did not show the
strong interaction effect seen with relative
body condition. This lack of direct correla-
tion 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 exper-
imental design, all hangars were stocked
with 20 individuals. Thus, when L. lugubris
in the presence of H. frenatus, its
intraspecific density was reduced by half
(from 20 to only 10 L. lugubris plus 10 H.
F. frenatus). Consequently, our design was a
conservative one, predicting more severe intraspecific
competition because we simultaneously re-
duced intraspecific competition in two-spe-
cies treatments.

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Cosymbotus platyrurus, Hemiphractylus ty-
pus, Gehyra mutilata, Gehyra oceanica, and other
sexual lugubris species) throughout the Pacific
shows significantly higher gecko densities on
buildings with electric lights than on those without
(APEX, 1987), with light and geographic area as
factors, light is significant at P = 0.03 (3).
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(1972).
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
inulation. Before the start of the experiment, all
geckos naturally occupying the hangars were
removed. The number of each species 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. garnoni.
We photographed the density of the
bunkers in several ways. A rope 2 cm in diameter
was string 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. Eighty 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 plywood; the top 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 the elimination of stimulants
for the range of gecko body size used in the experiment.
A second layer of black carpet was then attached
to the top of the plywood layer with Velcro. To
take censuses, we folded up the carpet and viewed
the geckos through the Plexiglas. A small wire
was then used to separate the geckos at the rear.
Geckos had free access to water throughout the experi-
ment. They were confined within hangars by the
use of Fluon AD-1 (Northern Products, Woon-
socket, RI), a silicone-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. A second Geckoflap was nailed to
the asphalt floor and also coated with
Fluon. In the enclosure, an additional stripe of
Fluon was painted on the wall to facilitate census-taking. Mammalian predators (females and mongos) are common on
the site and were excluded from the hangs by
placing traps. Because the area was patrolled regularly
by security guards, human interference was kept
below 1% per month. The full experiment ran from
12. To stock the experiments, we collected adult
geckos from several areas where they are
common and were raised in the laboratory.
We collected H. frenatus at Waikato on the north
shore of Oahu, whereas most L. lugubris were
collected from Haumalu Point (northern end)
side of Oahu and from Hilo on the windward
side of Hawaii. Geckos about to lay eggs or
appearing unhealthy were excluded. A subsam-
ples of each species were tested for the presence of
blood and gut parasites. We found no blood
parasites after examining Geamsa-stained blood
smears. A few (<50%) of the geckos examined had
a coccidiosis in fecal samples and cestodes or nem-
atodes in their guts (K. Hanley, unpublished data).
We marked the geckos by clipping off the
ends of their toes in an identifiable pattern (2) and
by painting recognizable patterns on their backs with
water-based paint (3).
13. The B-W fluorescent lights were controlled by a
system of 12-VE deep-cycle batteries and photo-
sensitive switches that automatically turned the
lights on and off to keep the geckos in daily
rhythm were replaced approximately every 8 days. No other
electric lights were present within a perimeter of at
least 1 km. The full experiment ran from
14. Gecko weight was measured to the nearest 0.1 g,
and snout-vent length was measured to the near-
est 0.5 mm. Eggs were counted and scored as
nones, small (<5 mm), medium (5 to 8 mm), or
large (>8 mm). Tail condition was judged by the
proportion of tail present (by weight). All indivi-
duals with <50% tail present or with tails 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 cater-
gories was given a crude weight index that reflected its
qualitative range. B-C, a category of bumble
wasp (the body wap of a bee) was scored as
<0.1. Data included here represented a range of
0–4. 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 mea-
sures, although the same trends and conclusions
were produced using raw counts.
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 that are generalized on
measures of demographic success (such as con-
dition) are highly correlated with numerical
changes in abundance in our 5-year study of
the same gecko species in Fiji (4) and with measures
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Two Open Complexes and a Requirement for Mg$^{2+}$ to Open the $\lambda P_R$ Transcription Start Site

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Potassium permanganate (KMnO$_4$) footprinting in the absence and presence of magnesium (Mg$^{2+}$) at the $\lambda P_R$ promoter identified two different open complexes with Escherichia coli E. coli RNA polymerase (designated RP$_{\alpha}$ and RP$_{\omega}$). The single-stranded region in RP$_{\alpha}$ (formed in the absence of Mg$^{2+}$) was at most 12 bases long, whereas that in RP$_{\omega}$ (formed in the presence of Mg$^{2+}$) spanned at least 14 bases. Only in RP$_{\omega}$ 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 Mg$^{2+}$ in the formation of RP$_{\omega}$ from RP$_{\alpha}$, 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$_{\gamma}$), an intermediate closed complex (RP$_{\gamma}$) that involves a major conformational change in RNAP, and an open complex (RP) 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.

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.

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 m$^2$ 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).

Alphalividuals 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 combined, 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. For the species-specific 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-L. lugubris, 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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K MnO$_4$ 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 $\lambda P_R$ promoter deduced from kinetic studies, we probed the accessibility of pyrimidines in these complexes to oxidation by KMnO$_4$ in the presence and absence of Mg$^{2+}$. The Km MnO$_4$ 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 KMnO$_4$ in the presence and absence of Mg$^{2+}$ (Fig. 1D).

RNAP formed open complexes on supercoiled plasmid DNA at the $\lambda P_R$ promoter from 4° to 37°C both in the presence and in the absence of 10 mM Mg$^{2+}$ (Fig. 1). However, Mg$^{2+}$ enhanced KMnO$_4$ modification at many positions, especially at both boundaries of the open region where the ratio of KMnO$_4$ reactivity in the presence of Mg$^{2+}$ to that in the absence of Mg$^{2+}$ was in the range of 3 to 8 (Fig. 1D). Positions +1T and +2T, unreactive or weakly reactive with KMnO$_4$ in the absence of Mg$^{2+}$, became accessible to reaction with KMnO$_4$ in the Mg$^{2+}$-induced open complex. In a similar manner, a large enhancement of KMnO$_4$ reactivity at positions −1T and −12C was observed in the presence of Mg$^{2+}$. 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 KMnO$_4$ reactivity in the presence of Mg$^{2+}$ to that in the absence of Mg$^{2+}$ was ≤3 (12).

Together, these data indicate a significant difference in the open complex in the presence and absence of Mg$^{2+}$. In the absence of Mg$^{2+}$, the extent of strand

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