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Insects, vegetation, and the control of laughing gulls (*Larus atricilla*) at Kennedy International Airport, New York City

P.A. BUCKLEY* and MOLLY G. McCARTHY[†‡]
*US National Park Service Coastal Research Center, Department of Natural Resource Sciences, University of Rhode Island, Kingston, Rhode Island 02881 USA; and [†]Graduate Program in Ecology, Rutgers University, New Brunswick, New Jersey 08903 USA

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Summary

1. In response to a purported 'bird-strike problem' at J.F. Kennedy International Airport in New York City, we examined short (5 cm) and long (45 cm) grass heights as gull deterrents, in a randomized-block experiment.
2. Vegetative cover, numbers of adult insects and of larval beetles (suspected on-airport food of the gulls) were sampled in the six-block, 36-plot study area, as well as gut contents of adult and downy young gulls in the immediately adjacent colony in the Jamaica Bay Wildlife Refuge.
3. We found that (i) Oriental beetle larvae were the most numerous and concentrated in one experimental block; (ii) beetle larvae numbers were uncorrelated with grass height; (iii) adult beetles were also uncorrelated with grass height; (iv) laughing gulls were distributed across blocks irrespective of percentage cover; (v) within blocks, laughing gulls were selecting short grass and avoiding long grass plots; (vi) laughing gull numbers were positively associated with numbers of Oriental beetle larvae; (vii) adult laughing gulls on the airport were eating lower-nutrition food of terrestrial origin (74–83% adult beetles, mostly Oriental plus green June and ground beetles); (viii) on the other hand, gull chicks in the adjacent breeding colony were being fed more easily digested, higher-protein food of marine origin (86–88% fishes, crustacea and molluscs); (ix) laughing gulls on the airport were taking their adult beetles only in short-grass plots, ignoring large numbers in adjacent long grass; (x) during the summer, on-airport gulls shifted from performing largely maintenance activities on pavement to feeding actively for beetles on newly mown short grass, the change coinciding with adult beetle emergence; (xi) standing water on the airport attracted significantly more gulls than dry areas all summer long.
4. We recommend a series of ecologically compatible, but aggressive habitat management actions for controlling laughing gulls on Kennedy Airport by rendering the airport unattractive to them, notably by implementing an airport-wide programme of long-grass encouragement, draining standing water and improving run-off in water-collecting areas, and controlling beetles.
5. We conclude by outlining the necessity for airport-wide bird, vegetation and habitat management programmes fully integrated into airport operation and planning activities.

Key-words: beetles, bird-control, bird-strikes, grass-height, integrated pest management.

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[‡] Present address: Department of Biological Sciences, The Ohio University, Athens, Ohio 45701, USA.

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Introduction

Laughing gull, a near-obligate saltmarsh-nesting North American endemic, was extirpated in 1900 as a breeding bird from Long Island, New York, USA by plume trade depredations. Subsequently, despite extensive range recolonization as close to New York as southern New Jersey (150 km), whose population had recovered to 35 000 pairs by 1977 (Buckley 1979), recolonization of Long Island did not occur until 1979 when 15 pairs were found in *Spartina–Distichlis* in the JoCo Marsh section of Jamaica Bay Wildlife Refuge (JBWR), a unit of Gateway National Recreation Area, a US National Park. JoCo marsh is immediately adjacent to the southwest end of 4L/22R, one of the busiest runways at John F. Kennedy International Airport (JFKIA; Fig. 1). The JBWR colony grew rapidly by recruitment from southern New Jersey colonies, and by 1983 had reached 1805 pairs (Buckley & Buckley 1984).

Since its inception, JFKIA has had a problem with water and grassland birds attracted to its flat, open spaces, undisturbed grasslands, and occasionally enormous, shallow rainwater pools — all habitats increasingly scarce in the metropolitan New York City area. After the crash of a DC-10 in 1975 following collision with several feral Canada geese (*Branta canadensis*), JFKIA established a bird-control unit to keep runways free of birds during daylight hours. The patrol also collected carcasses of birds found dead on JFKIA operational areas, all such birds being considered 'bird-strikes' by definition, irrespective of cause of death, which was rarely if ever determined by post-mortem. It appears that the first dead laughing gull was found on JFKIA sometime in the 1970–78 period; two were found in 1979 and numbers increased gradually until 1984, when 60 were found (S. Chevalier, JFKIA Bird-Control Unit, personal communication). Thus, even though few irrefutable aircraft–laughing gull collisions (true bird-strikes) had been reported, in 1984 the Port Authority of New York and New Jersey (PANYNJ) expressed disquiet about their 'laughing gull problem'. Increasing numbers were being seen bathing and drinking, feeding and forageing in public areas (parking lots, food concessions, lawns, roadside edges) and operational sections (taxiways, runways, access roads, sewage treatment plant). Many of these sites were characterized by landscaping grass regularly cropped to lawn-height, or naturally sparse, low-cover vegetation (frequently also grasses), as well as by standing freshwater — all well-known gull attractants in coastal areas. In addition, after heavy rains, gulls of several species would collect at rainwater pools on the airport, often by the thousands (personal observation).

In the early 1980s, flocks of laughing gulls had begun to congregate in mid June at various grassy locations in operational areas of the airport, especially between runways 4L/22R and 4R/22L (Fig. 1), where they appeared to be catching insects both in the air and on the ground. At the same time large numbers of Japanese beetles (*Popillia japonica*) were trapped in passenger and cargo areas, so airport officials concluded these insects were attracting the gulls. Concerned about beetle-eating gulls posing a hazard to aircraft, and enough beetles to cause the US Department of Agriculture to declare JFKIA a 'regulated' airport (requiring internal spraying of all incoming flights and elaborate quarantine measures), it was suggested that aerial spraying of all airport grounds would solve both beetle and gull problems simultaneously. Worried about the environmental effects of large-scale pesticide application in an estuary largely protected as a National Park, airport authorities approached the first author about undertaking a research study that might provide an alternative solution.

Because laughing gulls are migratory at JBWR, being present only from about April to October, and largely feed on fish and marine invertebrates, we suspected that their summertime presence on JFKIA represented opportunistic use of insect food and freshwater supplies. Based on earlier work manipulating grass height to reduce airports' attractiveness to birds (e.g. Brough & Bridgeman 1980), we also suspected that vegetation management would provide a solution to JFKIA's perceived laughing gull and Japanese beetle problems compatible with both airport and park interests.

Dominant insects taken by gulls on JFKIA all proved to belong to the family Scarabaeidae, and in the subfamily Rutelinae included Japanese beetle and Oriental beetle (*Anomala orientalis*); in the subfamily Melolonthinae, Asiatic garden beetle (*Maladera castanea*) and European chafer (*Amphimallon majalis*); and in the subfamily Cetoniinae, green June beetle (*Cotinus nitida*), the only member of the group native to North America.

All five insects are univoltine, adults ovipositing in summer in soil, where larvae feed on plant roots and decaying vegetation; in late fall the larvae burrow to a depth of 20–25 cm, where they overwinter. Early the following spring they move back towards the surface, feeding until pupation in late spring. Emergence of four of the five species normally occurs in June and July (green June beetle about a month later), annually tuned by temperature and early spring precipitation (Metcalf & Flint 1962).

Of the five, the green beetle is largest, averaging 18–24 mm long and 9–11 mm wide; the remaining four are between 8–12 mm wide and 4–6 mm long, with the Oriental beetle smallest and Japanese beetle largest. They are all considered pests, feeding diurnally as larvae (all) or as adults (all but European chafer) on lawns, golf courses, gardens and orchards. The sandy, vegetated and often moist soil of JFKIA

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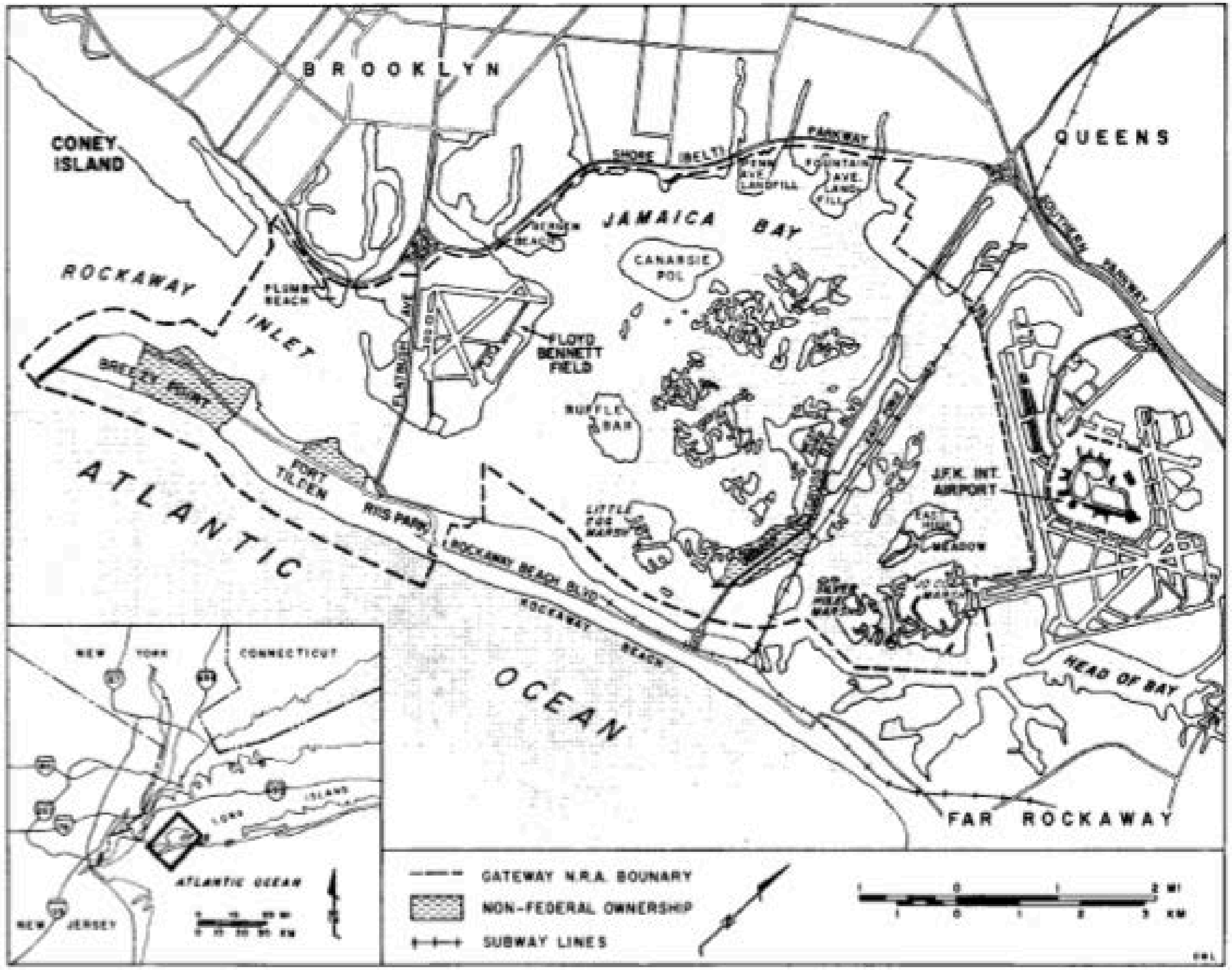

Fig. 1. Locator map of Gateway National Recreation Area, Jamaica Bay Wildlife Refuge, and Kennedy International Airport, in the Boroughs of Brooklyn and Queens, New York City. Note the JoCo Marsh laughing gull breeding site, off the end of JFKIA runway 4L/22R. Immediately below it (just above 'Head of the Bay') is the experimental site ('between the 4s').

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thus provided excellent breeding conditions for all five species and even though green June beetle larvae were not detected in our study plots in either year, they could easily have bred elsewhere on JFKIA.

Methodology and design

Adult and larval insect abundance, and laughing gull numbers and feeding, were contrasted throughout two summer breeding seasons (1985 and 1986) under short and long grass experimental regimes. Our major null hypotheses were that (i) larval and adult insect abundances were equal in short and in long grass; and (ii) laughing gull use was equal in short and long grass. We also sampled crop contents of adult gulls foraging on the airport, and food boluses from chicks in the colony, thus null hypothesis (iii): adults on the airport and chicks in the colony would be consuming the same kinds of food in the same proportions. Lastly, detailed observations were made on numbers and behaviours of laughing gulls on the airport relative to wet and dry areas, whenever we found them during the periods of study, viz. 1 April–30 September, especially in 1986, thus null hypothesis (iv): gull use of the paved portions of airport was independent of standing water occurrence.

Because initial observations had shown most laughing gull activity to occur in the 225 ha grassy area between runways 4L/22R and 4R/22L ('between the 4s') we chose that area for our experimental grass plots (Figs 1 & 2). Other data were collected anywhere within the operational areas of the airport, and occasionally in public areas as well. The study was originally formulated as a multilevel, randomized-block experimental design involving several variables: short and long grass, application of milky spore disease (*Bacillus popilliae*) to control beetle larvae before emergence, and ground application of a selected chemical control agent for beetles. However, a major influx of beetles into cargo and passenger areas in July 1985 resulted in a no-warning, blanket aerial insecticide spraying of the entire airport, obviating this experimental design. As this occurred after the grass plots had been cut, the study was redesigned to use grass height as the only experimental variable. Since the airport's establishment in the 1940s, aerial and ground spraying had been periodically done, so the July 1985 application of malathion reflected an almost regular occurrence.

GRASS-HEIGHT PLOTS

Plots with grass heights, of approximately 5 cm (short) and 45 cm (long) were established, as suggested by earlier studies (e.g. Blokpoel 1976; Brough & Bridgeman 1980). Three plots of each treatment were replicated six times, in a randomized-block design, for a total of 36 experimental plots in six blocks; long and short grass treatments were randomly allocated to three plots in each of the six blocks (Figs 2 & 3). Each 0·4 ha plot was a square 63·6 m on a side; the outside dimensions of each of the six replicate blocks were 291 m × 177 m (5·2 ha); and the experimental array occupied *c.* 31·2 of the 225 ha. Areas outside treatment blocks remained uncut, except for a 50 m wide buffer zone of uncut grass maintained between each plot to minimize contamination effects and to reduce the chance of biasing the attractiveness of the site to laughing gulls. Grass height in uncut areas varied from approximately 5 cm to 2 m.

Plots were surveyed in April 1985, short-grass

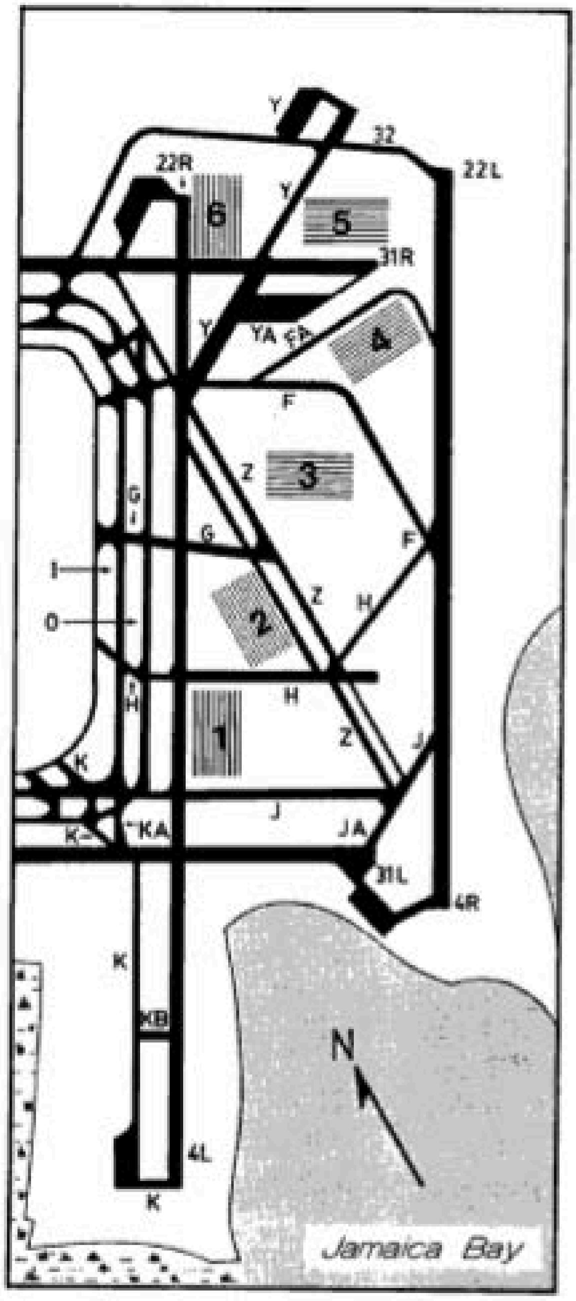

Fig. 2. Detailed airport map of the experimental site, showing the six numbered experimental blocks, each of which contained six plots of short and long grass. Paved taxiways are in black, and JoCo Marsh is just below taxiway Kilo (K) at the bottom of the figure. Runways are numbered, taxiways lettered. Asterisks indicate the top of each block, for orientation in Fig. 3.

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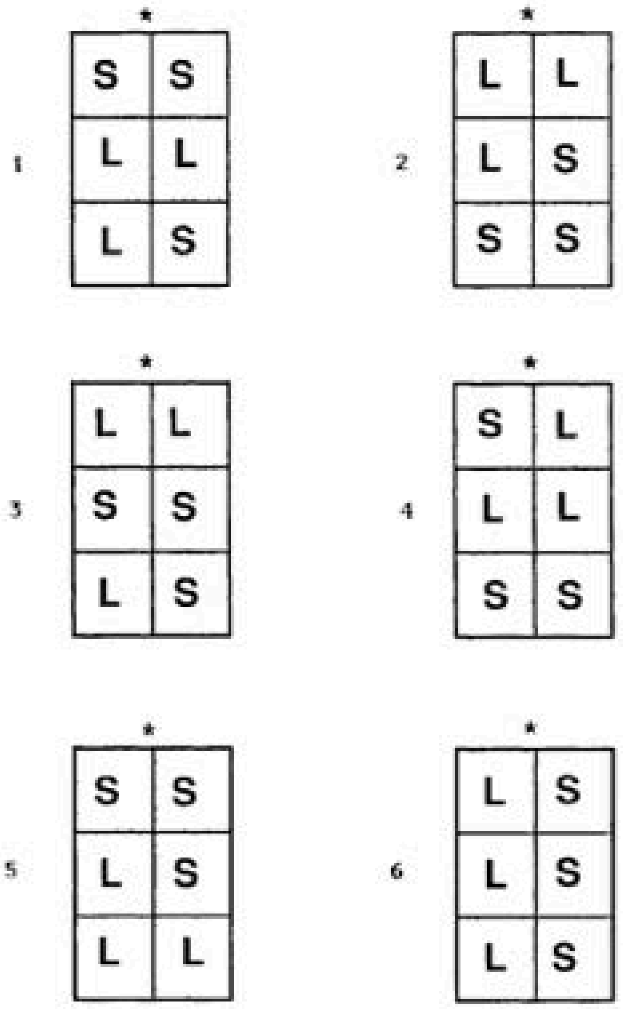

Fig. 3. Schematic configuration of short- and long-grass plots in each experimental block. Asterisks at the top of each block conform to those in Fig. 2. Not depicted are the 50-m buffer strips between (only) each separate plot.

plots were mown 22–27 May 1985, and long-grass plots 28 May–3 June 1985. To maintain treatment heights, all plots were recut between 8–12 July, 14–16 August and 17–20 September 1985.

VEGETATIVE COVER

Percentage cover of vegetation in each of the 36 short- and long-grass experimental plots was recorded using a $0{\cdot}25\,m^2$ point-sampling frame (Mueller-Dombois & Ellenberg 1974). Plant species occurring under each of the 25 points of the frame created by 10 crossed wires were recorded. Each plot was sampled in six locations, for a total of 216 samples. To achieve maximum cover estimates, sampling was conducted between 20 and 25 September 1985, toward the end of the growing season and after a recent cut of all plots. Thus, each block's percentage cover value came from 18 short- and 18 long-grass plot samples.

INSECT OCCURRENCE AND ABUNDANCE

Larvae

Surveys of beetle larvae in all 36 study plots were conducted in June 1985 to determine the distribution, composition and expected abundances of adult beetles during the primary study season. Larvae were selected because they are stationary in the soil and can be associated with specific plots. As beetle distribution is known to be aggregated (Ng, Trout & Ahmad 1983), stratified random sampling was employed. Plots were divided equally into fou quadrats and each of these quadrats was randoml subsampled. One $30\text{-}cm^2$ sample of soil in each quadrat was removed to a depth of 15 cm, for a total of 144 samples. Larvae were extracted using soil sieves, and returned to the laboratory for identification. Larval sampling was repeated in May, 1986 (no plots had been cut since the previous autumn) to determine any variation between years, and to see if a season of grass height manipulation had any effect on ovipositing beetles, a possible management complication.

Adults

Adult insects of all kinds were monitored in the plots from 25 July to 24 August 1985 using six traps placed in each of the 36 plots for a total of 216 traps. The traps were $25\text{-}cm^2$ plexiglass plates covered with clear contact paper to which was applied 'Tanglefoot', a sticky material that entangles insects landing on it. Insects on each trap were counted and identified every 6 days, at which time traps were changed and relocated; 1075 traps were sampled in all.

LAUGHING GULL USE OF EXPERIMENTAL PLOTS

After all plots had been cut to the required length, gull data (numbers, age-classes, and behaviour such as foraging, feeding and maintenance activities, especially bathing and drinking) were taken at each plot every third day from 23 June to 17 August 1985. By the latter date most fledglings and adults were no longer coming regularly onto the airport, except to join hundreds of other birds at rainwater pools on paved surfaces after heavy rains. Sampling was done between 06.00 and 20.00 h, in numerical order by plot and block, beginning with block 1 on the first sampling day. In order to avoid position effects or bias from diel differences in behaviour or activity, the order of plots sampled was rotated, each day's sampling starting at the plot sampled second during the previous run. If no gulls were present 5 min were spent at each plot; if gulls arrived, data were taken for an additional 5 min.

Grass height in experimental plots could not be maintained beyond 1985, so in 1986 we made a pseudo-random sampling of all species of gulls encountered on the airport, augmented by casual observations by the JFKIA bird-patrol team. Flocks were recorded on standardized airport maps, along

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with date, time, numbers, species composition, habitat type (grass, other vegetation, wet pavement, dry pavement, etc.), and behaviour. No time limits were imposed at each data point.

FOOD TAKEN BY GULLS

A total of 37 volant laughing gulls either found dead on the airport or shot by the bird-patrol were salvaged for dietary analysis in both years. Carcasses were frozen whole and stored for post-field season analysis, at which time they were allowed to thaw; their crop contents were then removed and weighed. Food items were sorted as animal, vegetable or inanimate. Animate matter was further subdivided down to recognizable levels: to species or families in the case of beetles, occasionally only to phylum or class for other organisms. Prey were categorized by percent wet weight.

Fifty chicks were likewise sampled over the 2 years, by taking regurgitated bolus samples from them at widely scattered locations throughout the 2-km^2 marsh colony site. Chick food items were categorized by percentage volume in 1985, and by percentage wet weight in 1986. While absolute values were thus not strictly comparable between years or age-classes, the analyses were done on ranked data (see below) and rank order by volume was probably similar to rank order by wet weight (H. Ginsberg, personal communication) Thus, many comparisons could be validly made.

STATISTICAL ANALYSES

We generally chose powerful nonparametric tests for our data analyses, rather than risk the weakened probability inferences attendant on using parametric tests with data differentially departing from rigid assumptions. All tests were done in the SAS system (version 5.0) on an IBM mainframe (SAS 1985).

Because most of the nonparametric tests we used were done on the ranks of the original data, no other transformations were necessary. Percentage cover data were not arcsin transformed, as few extremely high or low values were obtained. For ease of significance estimation, certain test statistics were expressed as Z-values (standardized normal deviates).

For comparisons involving only two treatments, such as the effect of grass height on the presence of laughing gulls or beetle larvae, or differences in prey selection between adult laughing gulls and chicks, we used the Wilcoxon two-sample test (equivalent to the Mann–Whitney test). When contrasting differences among blocks, such as for beetle larvae and percentage cover, we used multivariate rank tests (SAS 1983, p. 361), similar to Kruskal-Wallis one-way ANOVA on ranks. Parametric ANOVA was used to test for differences in adult insect densities by block or by grass height. If ANOVA-type tests indicated differences somewhere between blocks, these were located by Tukey-type nonparametric multiple comparison tests (Zar 1984, p. 199), or, in the case of the insect density data, by a parametric Tukey multiple comparison test (Zar 1984, p. 189).

To analyse the effect of numbers of scarabaeid beetle larvae on numbers of feeding laughing gulls, a chi-square test was performed on a 2 × 2 contingency table based on presence/absence data. For this analysis, only data on laughing gulls in the plots during June 1985 were used, corresponding to the time of larval sampling. Chi-square tests were also used to compare differences in laughing gull numbers on grass and pavement, and Spearman rank correlation to test for association between laughing gull numbers in the plots and their vegetative cover.

Results

VEGETATION AND COVER

While there were statistically significant (but for our purposes immaterial) differences in plant species composition among blocks, switch grass (*Panicum virgatum*) and beard grass (*Andropogon scoparius*) were the co-dominants in all blocks save block 3, where asters (*Aster*) predominated. Block 3 also had the greatest proportion of unvegetated area (35·0%), largely sand and small rocks. Mean percentage cover varied little among blocks, but block 3 had significantly less cover than blocks 1, 2 and 4, and block 6 had significantly less than block 1 (Table 1). Despite these differences, percentage cover was uncorrelated with laughing gull abundance in all plots ($n = 36$, $r_s = 0{\cdot}16$, $P = 0{\cdot}68$), ignoring grass height.

LARVAL BEETLES

In both years, the most prominent beetle groups in the larval samples were various scarab beetles (Scarabaeidae; 81% in 1985 and 98% in 1986). Ground beetles (Carabidae) were second most numerous in 1985 (16% of larvae), but along with a handful of tiger beetles (Cicindelidae) and darkling beetles (Tenebrionidae) in both years, were almost absent in 1986. At the family level, only ground beetles occurred in significantly different larval numbers in 1985 and 1986.

Oriental beetle accounted for 80% of all scarabaeids in 1985 and 83% in 1986: — it was clearly the dominant beetle in our study plots, and thus the most likely insect food for foraging laughing gulls. Strikingly less numerous were Asiatic garden beetle, Japanese beetle and European chafer (Tables 2 & 3). Across blocks, there were significant differences in numbers of various scarabaeids within each year (Table 2), although not of the 1985 ground beetles

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Table 1. Summary comparisons of numbers of adult laughing gulls, numbers of beetle larvae, mean percentage cover, and mean adult insect density (number m^{-2}) for the six experimental blocks in 1985. Within each variable differences among blocks were tested by Kruskal-Wallis tests, except ANOVA was used for adult insect data. Within rows, values sharing a common letter superscript are *not* significantly different at the 0·05 level (Tukey-type multiple comparison tests)

	Blocks						
	1	2	3	4	5	6	
Total laughing gulls	6^{c}	457^{a}	19^{b}	0^{d}	0^{d}	0^{d}	***
Total beetle larvae	66^{b}	192^{a}	32^{b}	16^{b}	8^{b}	31^{b}	***
Mean percentage cover	$88{\cdot}5^{a}$	$83{\cdot}2^{ab}$	65^{c}	$84{\cdot}2^{ab}$	$79{\cdot}8^{abc}$	$70{\cdot}3^{bc}$	*
Mean adult insect density	$222{\cdot}4^{a}$	$146{\cdot}3^{c}$	164^{bc}	$186{\cdot}3^{bc}$	92^{d}	$75{\cdot}2^{d}$	***

* $P<0{\cdot}05$; *** $P<0{\cdot}001$.

Table 2. Summary of 1985 (upper) and 1986 (lower) distributions of numbers of scarabaeid larvae by blocks across JFKIA experimental sites, analysed by a Kruskal-Wallis multiway test. Within species, blocks with the same letter are *not* significantly different (Tukey-type multiple comparison tests). Statistical comparison between the two years is unimportant. Twenty-four samples were obtained from each block each year

	Blocks						
Species	1	2	3	4	5	6	Totals
Oriental beetles	14^{a}	172^{b}	8^{a}	4^{a}	3^{a}	27^{ab}	228
European chafers	0^{a}	0^{a}	1^{a}	0^{a}	1^{a}	0^{a}	2
Japanese beetles	2^{a}	10^{b}	0^{a}	0^{a}	1^{a}	0^{a}	13
Asiatic garden beetles	36^{a}	0^{b}	5^{b}	0^{b}	0^{b}	1^{b}	42
Totals	52	182	14	4	5	28	285
Kruskal-Wallis $\chi^2 = 54{\cdot}4$, df = 20, $P<0{\cdot}0001$							
Oriental beetles	18^{b}	208^{a}	8^{b}	16^{b}	19^{b}	37^{ab}	306
European chafers	0	0	0	0	0	0	0
Japanese beetles	2^{a}	2^{a}	0^{a}	1^{a}	8^{a}	2^{a}	15
Asiatic garden beetles	15^{a}	5^{a}	15^{a}	2^{a}	2^{a}	10^{a}	48
Totals	35	215	23	19	28	49	369
Kruskal-Wallis $\chi^2 = 46{\cdot}6$, df = 20, $P<0{\cdot}0001$							

Table 3. Comparison of Ground beetle larvae numbers by experimental blocks in 1985 and 1986. Within each year, no interblock differences were significant; between years total numbers on the experimental site did differ (Wilcoxon two-sample test, $Z=6{\cdot}03$, $P<0{\cdot}001$, $n=144$ each year)

	Blocks						
	1	2	3	4	5	6	Totals
1985	14	9	18	11	3	3	58
1986	0	0	0	1	0	1	2
Totals	14	9	18	12	3	4	60

(Table 3). Of all beetles, only Oriental beetle occurred in biologically important numbers, and was most numerous in block 2 in both 1985 and 1986. Across all species, block 2 held 52% of all beetle larvae in 1985, and 59% in 1986; block 6 was second in both years.

Oriental beetle and Japanese beetle larvae were more numerous in short grass plots, and Asiatic garden beetles in long grass, these tendencies nearly reaching significance (no Wilcoxon two-sample Z exceeded 1·42, $P=0{\cdot}15$). Moreover, when plots that were short or long in 1985 were compared in 1986, no difference in numbers of Asiatic garden, Oriental, Japanese, ground or tiger beetle larvae were found (no Wilcoxon two-sample Z exceeded 1·42, $P=0{\cdot}15$), confirming that grass length in 1985 had no differential effect on oviposition or on larval survival into the next year.

ADULT BEETLES AND OTHER INSECTS

Among adult insects known to have been eaten by laughing gulls at JFKIA in 1985, only Japanese beetles and ground beetles were unequally distributed among blocks, but they occurred in numbers too small to be meaningful. On the other hand, Asiatic garden beetles occurred in all blocks and were extremely numerous in block 1, but none were eaten by adult gulls in 1985. Other insects were also distributed unequally, but were also barely (if at all) taken by gulls. Nonetheless, across all insect groups, total density (number per m^2) was significantly lowest in blocks 5 and 6 (Table 1).

Adult insects also generally showed no preferences for short- or long-grass plots. Those that did were more abundant in long grass, and again none were important in the gulls' diet in 1985. Table 4 summarizes block and grass height preferences for all abult insects in 1985.

LAUGHING GULLS AND THE EXPERIMENTAL PLOTS

The largest number of laughing gulls recorded in any study plot in 1985 at any one time was 75, with a cumulative seasonal total of 482 across all six blocks. This almost certainly includes repeat observations of the same individuals. Of the 482 birds, 95% or 457 were in block 2, and we never recorded any in blocks 4, 5 and 6 (Table 1). More importantly, however, within blocks, the distribution between short- and long-grass plots in 1985 was also skewed: 468 in short, 14 in long (Wilcoxon two-sample

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Table 4. Summary of statistically significant block-distributions (Kruskal-Wallis tests) or grass-height preferences (Wilcoxon signed-rank tests) of adult arthropods captured on the JFKIA experimental sites in 1985

Organisms	Unequal distribution among blocks?	Grass-height preference?	Eaten by laughing gulls in 1985?
Japanese beetles	Yes*	No	Yes
Asiatic garden beetles	Yes**	Long*	No
Ground beetles	Yes*	No	Yes
Hemipterans	Yes**	Long**	No
Arachnids	Yes**	No	No
Odonates	No	Long**	Yes
Orthopterans	Yes**	Long*	Yes
Lepidopterans	Yes**	No	No
Hymenopterans	Yes**	No	Yes
Dipterans	No	Long*	Yes

* $P<0{\cdot}05$; ** $P<0{\cdot}01$.

$Z=4{\cdot}16$, $P<0{\cdot}001$), clearly falsifying our grass-height null hypothesis.

Among beetles, only numbers of larvae of Oriental beetles were significantly associated with laughing gull numbers in the experimental blocks in June 1985 (Table 5; $\chi^2=4{\cdot}39$, df = 1, one-tailed $P=0{\cdot}039$), a finding mirrored in the diets of adult laughing gulls on the airport in 1985 (see below).

In 1986, during our intensive on-airport gull censusing, JFKIA continued its normal practice of maintaining the grass in all operational areas at *c.* 5 cm heights, except our 1985, 225-ha experimental site between the 4s, which they left uncut. Consequently, laughing gulls and other species came onto grassy as well as unpaved areas of the airport in numbers; their selection of habitat was revealing. Early in our censusing, before 13 June, we found 69 laughing gulls on paved operational areas, but none in grassy areas which had not yet been cut from the year before; in the period 19 June–7 July, even though we still found 130 on pavement, there were an additional 279 actively foraging in recently cut, short grassy areas. These different proportions were highly significant ($\chi^2=110{\cdot}3$, df = 1, $P=0{\cdot}001$). We had predicted such a shift in habitat selection for two reasons: it coincided with both the 1985 period of maximum adult beetle emergence and with newly mown, very short grass. Further analysis of our 1986 census data confirmed another of our 1985 anecdotal-data conclusions: the importance of standing water on pavement as an attractant to area laughing gulls. In 1986, of 246 laughing gulls on pavement, 155 were in areas of standing water, and only 91 on dry pavement (many not far from flocks at pools), a highly significant imbalance ($\chi^2=16{\cdot}6$, df = 1, $P=0{\cdot}001$). Frequently-wet areas present in both 1985 and 1986 are shown in Fig. 4.

Table 5. Numbers of adult laughing gulls associated with numbers of Oriental beetle larvae in the experimental area in June 1985

	Adult gulls		
	Present	Absent	
Beetle larvae			
Present	7	43	50
Absent	4	90	94
	11	133	

PREY TAKEN BY LAUGHING GULLS

Adult gulls feeding on the airport in both 1985 ($n=18$) and 1986 ($n=19$) consumed mostly beetles (83% in 1985, 74% in 1986), with the balance divided among isopods, crustaceans, fishes and molluscs, the actual proportions differing slightly between years (Table 6, bottom). Chicks in the colony, on the other hand, were fed mostly on crustaceans, molluscs and especially fishes — totalling 88% in 1985 ($n=26$), and 86% in 1986 ($n=24$) — with the balance of their diet being beetles and other insects (Table 6, top). The diets of the two groups were thus almost totally reciprocal to one another.

If individual prey items or classes are contrasted between chicks and adults, and compared across both years (Table 7), the importance of marine-based food in the chicks' diet is highlighted. In addition, variation in the largely terrestrial prey items taken by adults on the airport (or possibly elsewhere) in the two years is evident: Asiatic garden beetles were absent in 1985, but important in 1986, and the reverse was true for green June beetles. Chicks were also fed differentially in the two years, receiving 18% crustaceans in 1985 and none in 1986, 7% ants in 1986 and none in 1985.

Overall, adult diets in both years differed biologically from those of chicks; the great interyear differences in diet within adults, and within chicks, are most safely ascribed to differential prey availability in the two years.

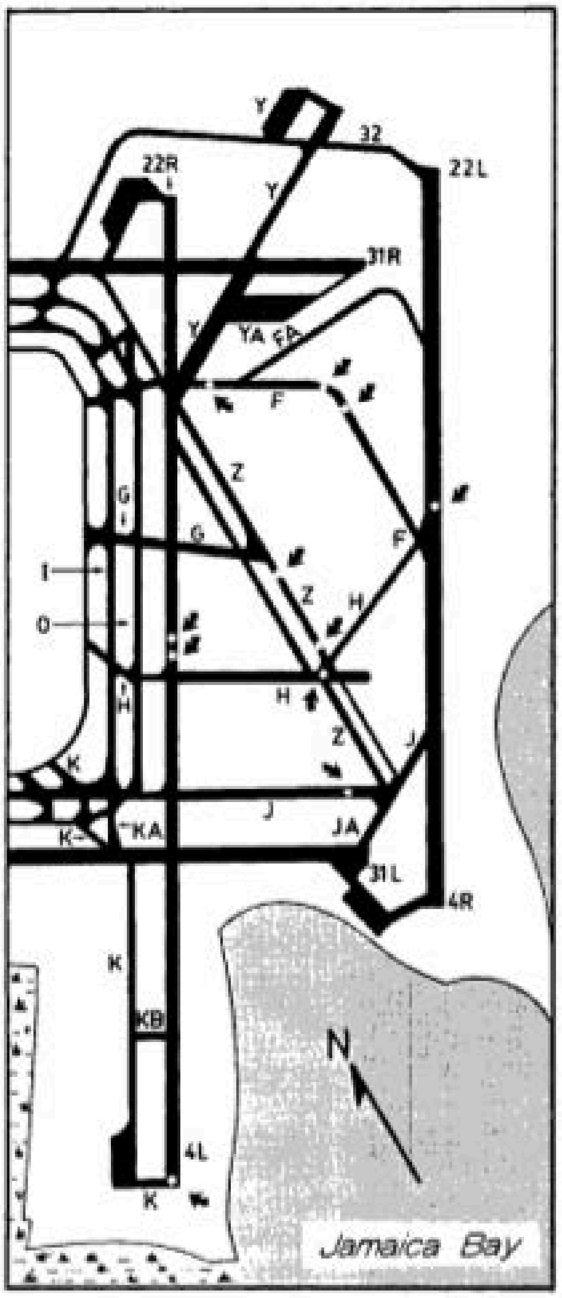

Fig. 4. The same base map as Fig. 2, now showing areas of regularly standing water on paved areas in the vicinity of the 4s that routinely attracted Laughing and other gulls in both 1985 and 1986. Arrows point to stars indicating the ponding sites; note how many are actually on runways 4L/22R and 4R/22L.

Discussion

The proximity of the experimental blocks to the laughing gull breeding colony in JoCo Marsh was unlikely to have been a factor in their on-airport distribution pattern, supported by the low use of block 1, the one closest to the colony. Proximity to runways was also not a factor, as runway activity varied hourly and daily with changes in weather and wind direction. Finally, because of the uniform experimental treatment of all blocks, and the absence of meaningful differences in percentage cover or vegetation types, those factors can also be ruled out as playing major roles in the observed non-random laughing gull distribution among blocks. But the distribution of beetles, especially Oriental beetle, showed a clear relationship to the distribution of laughing gulls.

Oriental beetles, not Japanese beetles, constituted the largest proportion of the diet of airport gulls, and these beetles were most numerous in block 2. (It should be noted that the distribution of Oriental beetle larvae was relatively uniform throughout block 2 in 1985, unaffected by grass length because oviposition had occurred in 1984 prior to controlled grass cutting.) But within block 2, laughing gulls avoided long-grass plots almost entirely, demonstrating that the attractiveness of Oriental beetles was important only in short-grass plots. In other words, the repellent effect of long grass alone to laughing gulls was almost totally effective, even in the face of abundant and easily obtained prey resources.

The prey items present in greatest proportions in the stomachs of laughing gulls in 1985, yet absent from the samples in 1986, were adult green June beetles. This species was never encountered in larval samples or on adult insect traps, although it was occasionally observed in swarms around the airport in late afternoon. It seems likely that laughing gulls were catching green June beetles adventitiously elsewhere, on or off the airport; in any event, they were unimportant in attracting laughing gulls to JFKIA. Moreover, the large percentage of green June beetles in the 1985 diet of airport gulls could have been an artefact of their large size, 2·3 times that of Oriental and the other scarabaeid beetles, so only a few individuals would have given disproportionately high percentages.

Asiatic garden beetles were the second most abundant beetle larvae in the experimental plots, concentrated in block 1. Adults were also common in block 1, and were occasionally found in stomach samples from laughing gulls, but it is highly unlikely that this species influenced the distribution of laughing gulls on the airport. Moreover, they were probably not regularly eaten because of their largely nocturnal habits.

Laughing gulls occasionally forage for soil invertebrates such as earthworms and insect larvae, but more commonly feed on adult insects. Indeed, in this study, all insects found in laughing gull stomachs were adults. Yet the results of the adult insect sampling at JFKIA failed to demonstrate significant associations between adult insects and airport laughing gulls. This may be due in part to two factors: (i) the frequencies of beetles (the most numerous prey item) encountered on the insect traps were too low to allow statistical discrimination of distributional differences, although more abundant insects such as grasshoppers, crickets, ants and dragonflies also showed no clear patterns of distribution: and (ii) after emergence, insects become highly mobile, making their distributional patterns more difficult to detect. So, even though most

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Table 6. Diets of adult laughing gulls on the airport, and chicks in the colony, in 1985 and 1986, contrasting the terrestrial diet of the former, and the marine diet of the latter, and demonstrating year-to-year compensation of individual dietary components as a function of annual availability. Adult data are percentage wet weight, as are chicks in 1986; chick data for 1985 are percentage volume. See text for discussion of comparing the two methods

	1985		1986		
Chicks					
Oriental beetles	4·3	12·0%	0	14·5%	Essentially *terrestrial* in origin
Japanese beetles	0·9		0		
Greenhead flies	5·5		2·8		
Other insects & miscellaneous items	1·3		11·7		
Fishes	55·6	88·0%	85·5	85·5%	Essentially *marine* in origin
Crustaceans	18·6		0		
Molluscs	13·8		0		
Adults					
Scarabeid beetles	70·0	92·8%	55·4	77·0%	Essentially *terrestrial* in origin
Ground beetles	9·5		18·6		
Tiger beetles	4·6		0		
Hymenopterans	3·2		3·0		
Othopterans	3·6		0		
Isopods	0	7·2%	10·0	23·0%	Essentially *marine* in origin
Crustaceans	0		10·0		
Fishes	3·6		0		
Molluscs	3·6		3·0		

Table 7. Diets of adult (1985, $n = 18$; 1986, $n = 19$) and downy young (1985, $n = 26$; 1986, $n = 24$) laughing gulls at JFKIA and JBWR, respectively. All data as percentage wet weight except 1985 chicks (percentage volume); see text for discussion. Analysis by one-tailed Wilcoxon two-sample test predicting adults eating terrestrial insects and chicks eating marine-based prey. Only significant age-class differences shown; see Table 6 comparing same age-classes across years

Prey	Year	Adults	Chicks	*Z*	*P*
Oriental beetles	1985	29·1	4·3	1·04	<0·05
	1986	44·0	0	3·18	<0·05
Green June beetles	1985	34·5	0	2·93	<0·05
	1986	0	0	—	—
Asiatic garden beetles	1985	0	0	—	—
	1986	11·4	0	2·61	<0·005
Ground beetles	1985	9·5	0	1·58	~0·05
	1986	18·6	0	1·76	~0·04
Tiger beetles	1985	4·6	0	1·58	~0·05
	1986	0	4·4	−0·84	NS
Othopterans	1985	5·5	0	1·58	~0·05
	1986	0	0	—	—
Greenhead flies	1985	0	5·5	−1·23	NS
	1986	0	2·8	−1·82	~0·035
Ants	1985	3·2	0	1·58	~0·05
	1986	3·0	7·3	−0·42	NS
Crustaceans	1985	0	18·7	−2·72	<0·005
	1986	10·0	0	1·08	NS
Fishes	1985	3·6	55·7	−4·46	<0·005
	1986	0	85·5	−5·42	<0·005

laughing gulls caught adult beetles in short grass, some were seen catching them well out on paved surfaces. Therefore, the stationary nature of scarabaeid larvae in the soil is a better mirror of gull–insect relationships. Several of the gull crops analysed were collected from birds shot while actively foraging in block 2, where Oriental beetle larvae were most numerous; predictably, these stomachs revealed large numbers of adult Oriental beetles. Additionally, peak laughing gull abundances on the airport occurred in late June and early July in both 1985 and 1986, also the time when they were most frequently encountered on airport grass, coinciding with Oriental beetle emergences. Even though

Japanese beetles also emerged at this time, they did not show up in stomach analyses in significant numbers and were uncommon as larvae. These data confirm the great importance of Oriental beetles in attracting laughing gulls to JFKIA, and the relative unimportance of Japanese beetles.

Although larval Japanese beetles were never abundant at JFKIA, adults were observed in large numbers at various airport sites during the summer months. Why, then, are they not exploited by laughing gulls to the same degree as Oriental beetles? A few differences between the two scarabaeid species may provide an explanation. (i) Body size: the smaller Oriental beetles may be easier to handle, swallow and digest. (ii) Activity patterns: Oriental beetles are more commonly encountered on the ground, while Japanese beetles are more active aerially. Laughing gulls do routinely hawk insects on the wing, but may prefer the accessibility of the ground insects. (iii) Numbers: because Oriental beetles are abundant as larvae, their emergences create very concentrated food supplies, whereas Japanese beetles are not emerging at JFKIA in large numbers and although abundant as adults, are more scattered in their distribution, so would not be captured as efficiently. (iv) Palatability: possibly aposematically coloured Japanese beetles might be distasteful to laughing gulls.

The proportions of insects in chick food boluses that could reasonably have been obtained at the airport were insignificant. Only 5% of prey items in chick boluses in 1985 consisted of Oriental beetles, the laughing gull's primary food resource at the airport, while there were no beetles of any kind present in boluses in 1986. The predominant food items in both years were fishes, a rich source of easily digestible protein. This suggests that, though abundant at the airport, insects were not of sufficient quality to support growing chicks. It appears that virtually all parent gulls foraging for chick food avoided the airport and, instead, obtained fishes and crustaceans in tidal areas, as laughing gulls usually do. Annett (1985) reported that for two other *Larus* species, *L. argentatus* and *L. occidentalis*, adults exploited predictable food sources during pre-laying and incubation, but once chicks hatched, switched to unpredictable, but higher quality food sources, such as fishes.

One major question, so far unanswered, concerned the importance of the airport as a food source for the entire Jamaica Bay laughing gull population. The cumulative number of laughing gulls at JFK in the experimental plots in 1985 was 482 which, even assuming no repeat individuals (a most improbable assumption), represented no more than 10% of the breeding population. No more than 75 were ever seen at one time in the plots, placing a lower limit on the number of individuals, and potentially an upper limit. While nests were not counted in 1986, the cumulative adult gull total on JFK that year was 548, still no more than 10% of the 1985 breeding population, again assuming no repeats. (The actual percentage for 1986 was likely to have been even less, since the breeding population that year appeared to have increased over the year before, but this is not certain). Thus, the proporti

of JBWR breeding laughing gulls feeding on otherwise using airport resources was small indeed. Moreover, there was no evidence suggesting that the 37 laughing gulls collected on the airport were nesting: none had enlarged gonads, although this is not an unusual post-egg laying condition for birds, and none had the evident brood patches typical of incubating laughing gulls (Noble & Wurm 1943). Both findings strongly suggest that those laughing gulls foraging at the airport were *not* current breeders. If true, then only a small, non-breeding proportion of Jamaica Bay laughing gulls was exploiting food resources at the airport, and the breeding population as a whole was not dependent on airport food.

Several beetle management considerations are evident. (i) Any insect control programme should account for their patchy spatio-temporal distribution by treating the whole airport as a unit, not just the parts of it that happened to have an insect population at a given moment. (ii) In addition to addressing adequate sampling regime, particular attention should be paid to quantifying beetle populations using metapopulation modelling techniques originally developed for insects (Levins 1969, 1970) and updated in a recent monograph (Gilpin & Hanski 1991). (iii) It is highly likely that, notwithstanding the admonition in (i), above, JFKIA cannot be considered an island unto itself; for examples, there is good evidence that Japanese beetles, at least, are venturing onto the airport from adjacent residential areas, and the most effective means of their control on JFKIA might be their interception by a network of strategically placed pheromone traps on the airport's periphery. This is not to imply that there is not already a major breeding population somewhere else on JFKIA; this remains unknown. (iv) The most successful long-term pest-insect control measures today usually involve Integrated Pest Management (IPM), not the blanket aerial spraying of insecticides practiced at JFKIA (see, for example, Apple & Smith 1976). In particular, ecological and economic analyses should be done of inoculating the entire airport, public as well as operational areas, with milky spore disease, which potentially could control several species of beetles simultaneously. Moreover, as Oriental, Japanese, Asiatic garden and European chafer are all exotic species, possible use of taxon-specific, non-native parasitoids should be considered in the overall IPM programme.

It would also seem reasonable that airport authorities undertake the following actions to eliminate the nuisance caused by laughing gulls: (i) extirpation

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of all permanent or quasi-permanent ponds of standing freshwater anywhere on the airport; (ii) improving drainage on the entire airport so that rainwater is immediately drained away; (iii) implementation of an airportwide IPM programme after airportwide censusing for potential insect foods for laughing gulls, ring-billed gulls (*L. delawarensis*) or other species of potential concern to airport operators; (iv) implementation of an airportwide programme of maintaining long grass in all suitable open areas; (v) planting and fertilizing of grass mixtures in all operational areas now in 'natural' vegetation but essentially bare or nearly bare. This might be done most effectively by hydroseeding; (vi) annual or biennial tall-height mowing of grassy areas on the entire airport in order to prevent grasses from succeeding to forbs, shrubs and trees that occlude aircraft visibility, can be a fire hazard, or present other problems to airport managers; and (vii) expansion and modernization of the JFKIA bird patrol to meet increased aircraft-operation and bird-occurrence needs, and to conform to contemporary international standards.

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