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Pharmacology Biochemistry & Behavior, Vol. 55, No. 3, pp. 339–349, 1996

0091-3057/96 $15.00 + .00

PII S0091-3057(96)00103-7

Lead and Behavioral Development: Parental Compensation for Behaviorally Impaired Chicks

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Received 1 September 1995; Accepted 9 February 1996

BURGER, J. AND M. GOCHFELD. *Lead and behavioral development: Parental compensation for behaviorally impaired chicks.* PHARMACOL BIOCHEM BEHAV **55**(3) 339–349, 1996.—Lead is ubiquitous in nature, and can affect behavioral, physiological, and intellectual development in humans and other animals. We used lead-induced behavioral deficits to examine the behavior of parents and young herring gulls in the Captree, NY, gull colony. Our objectives were to determine: a) If there were differences in the behavior, weight, and survival of chicks as a function of treatment; b) if parental behavior varied as a function of treatment; and 3) if there were differences in sibling competition and parent–young conflict between experimental nests (with lead-impaired chicks and control chicks) and control nests. We injected one chick in each of 22 nests (1–2 days of age) with lead acetate (100 mg/kg in sterile water) and injected its sibling with sterile saline, and compared behavior of parents and young (from 1–21 days postinjection). We also observed behavior of parents and chicks in 12 control nests in which chicks were handled similarly but were not injected. There were significant lead-induced differences in righting response, locomotion, thermoregulation, begging, and feeding behavior in the chicks; corroborating observations from the laboratory. Lead-injected chicks were less able to compete for food with their siblings, with a resultant significant difference by weight at 16 days of age. For experimental nests in which the weight difference was great, parents engaged in divided feeding of the brood. After one parent initiated feeding, the other parent walked a short distance away and began to call to and then feed the second, smaller chick. The extra parental care resulted in increased survival for the lead-injected chicks, and in their catching up to their siblings in weight by fledging. The results of this experiment indicate that lead induces behavioral deficits and growth retardation in gulls in nature, decreases survival at young ages, and that parents compensate for these behavioral and growth deficits by brood division for feeding chicks such that by fledging the chicks are no longer at a weight and size disadvantage. Parents are, thus, able to perceive a difference in body size and/or vigor of their offspring, and to behaviorally compensate partially for the lead-induced deficits. **Copyright © 1996 Elsevier Science Inc.**

Lead Birds Behavioral development Gulls Parental investment

RECENTLY there has been increased interest in assessing the well-being of animal populations, communities, and ecosystems. This has involved the combined efforts of biologists, toxicologists, and risk assessors (41–43). Usually behavioral, evolutionary, and other biological data have been used by risk assessors and managers to predict adverse outcomes of the exposure of organisms, populations, and communities to stressors or to solve particular environmental problems (42). Lead is still one of the most frequently encountered contaminants in the environment (3). Lead exposure in humans and other mammals may lead to neurobehavioral, hematologic, nephrotoxic, and reproductive effects, and developing infants and children are particularly vulnerable (1,5,35,38,39). The development of avian models to examine the effects of lead on the sensitive developmental period are critical not only to understanding the effects of lead on birds, but to serve as paradigms for further mammalian research.

In this field experiment we examine parental and sibling behavior in herring gull families in which only one sibling has been impaired by an injection of lead. We exposed chicks to concentrations of lead similar to levels young herring gull chicks can encounter in the wild in the population we studied

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(21,22). Presumably, this exposure is from a variety of foods provided by parents from local resources. Moreover, there are no other studies examining the effects of lead on completely wild young birds that are being cared for by free-living parents.

Herring gulls normally have a brood of two to three, and both parents incubate, feed chicks, and defend their offspring (9,10). The first two chicks usually hatch on the same day, and the 3rd chick hatches a day or two later. Normally, one parent guards the chicks while the second parent is away on a foraging trip. When the parent returns it feeds the chicks, and relieves its mate, which then flies away to forage or remains on the territory to sleep or participate in territorial defense (10,45,48). When undisturbed, herring gull parents and their offspring continue to use their nest site and natal territory until the chicks fledge at about 7 weeks of age (8).

In the laboratory, herring gull chicks injected with low levels of lead suffer a number of behavioral abnormalities that include deficits in locomotion, balance, begging behavior, thermoregulation, depth perception, and growth (11–13,20). Moreover, individual recognition is delayed in lead-injected chicks (17). These behavioral deficits should impair the ability of lead-treated chicks to avoid danger and to compete with siblings for food in the wild, and might lead to starvation and death (17). In this experiment, lead should induce behavioral impairments in these chicks, reducing their competitive ability with their control siblings. These behavioral changes (lower activity levels, less mobility, fewer vocalizations) might be detected by parents. This experiment allowed us to examine parental behavior toward chicks that differ in quality. We test the null hypotheses that: a) there are no differences in behavior and weight of lead and control chicks, b) there are no differences in parental behavior toward lead and control chicks, and c) there are no differences in fledging success between lead and control chicks.

METHOD

Subjects and Study Sites

Herring gulls were studied from May 20 to August 1, 1993, at Captree State Park, Long Island, in a colony of 1000 pairs of gulls nesting in the dunes. The colony site is about 30–60% vegetated with grass, herbs, and bushes, which provide protection for the chicks from predators and thermal stress. Gulls were observed in two separate areas where sparse vegetation allowed observation. No significant differences in behavior or survival were noted between the two areas (Kruskal-Wallis χ^2 tests), and data were combined for further analysis.

Two plots were selected for observation on the basis of phenology (having enough nests with eggs starting to hatch at the beginning of the study period to ensure an adequate sample) and observability (low enough density of vegetation so that nests could be observed from one location). Although 12 nests in one plot and 10 nests in another were selected for study initially, one pair moved their chicks deep into the grass and another pair spent most of the time behind dense vegetation. Therefore, all observations were made at 20 experimental nests. An additional six control nests in each plot were selected for observation. Nests were marked, but to avoid disruption of normal behavior we did not fence the nests, as chicks can injure themselves trying to escape fences, parents try in vain to draw chicks away from the fences, and fences impede normal movement and block access to cover (8,9).

Exposure

Nests were selected that had two young chicks and a recently hatched chick (wet) or pipping egg. The first two chicks had to be dry and fluffy (1–2 days old where day 1 is the day of hatching). Thus, the chicks in all the study nests were the same age on the same day of the study. Using a protocol approved by the University Animal Review Board, and under appropriate federal, state, and park permits, one chick from each of 22 nests was injected with lead acetate (100 mg/kg), and its hatched sibling was injected with an equal volume of normal saline solution. Lead acetate was used because it causes negligible acute mortality or effects. The lead level chosen was similar to the potential exposure young herring gulls can receive in the wild from food provided by their parents (21,22). All chicks were color banded and banded with U.S. Fish and Wildlife Service bands. All chicks (including chicks in the control nests) were weighed when they were banded. We alternated nests, with the oldest (heaviest) chick receiving the lead injection in one nest, and the second chick in the next. If there was a 3rd (and youngest) chick, it was handled and banded, but was not injected, and served as an additional control that did not receive lead. Each experimental nest contained one lead-injected and one (or two) control chicks. One researcher (MG) performed the injections and the color bands were randomized so the observer (JB) was blind to the lead-exposure status of all chicks.

Behavioral Observations

On each day observations usually were made from 0730–1030 h and 1500–1700 h at one study site, and from 1030–1500 h at the other study site, and this was alternated up to 21 days postinjection. Observations were made every day. The observer was 10–15 m from the nests in a blind. The colony is in a state park, and the gulls are adapted to the presence of people. No further observations were made until chicks were captured at 38 days postinjection, just prior to their normal fledging age. Three types of behavioral data were recorded: chick feeding behavior, adult provisioning behavior, and general health and behavior of the chick. A more extensive description of other behavioral impairments in nature are described in Burger and Gochfeld (19). Because we did not want to influence the behavior of parents or their chicks, we entered the study plots only three times during the experiment to weigh chicks (and record righting response, defined as the time required to right itself when placed on its back) on days 7, 14, and 38 days postinjection (when chicks were 9, 16, and 40 days old). At 16 days of age normal chicks still do not run very far from the nest, but thereafter the chicks would have scattered if we disturbed them. By 40 days of age chicks are nearly able to fly, and they are routinely moving about the colony (9).

Behavioral observations were made only until the chicks were 23 days of age to avoid undue disturbance. At this age herring gull chicks begin to move about frequently (9), and will run long distances if disturbed by people. Although we did not enter the colony to make our observations, we still wished to ensure that our presence did not alter subsequent behavior that might affect fledging success.

Chick feeding behavior was observed by two methods. At the start of every observation period we recorded a score for begging the first time each chick initiated feeding [see Burger (9)], and the number of times it missed (or hit) its parents bill when pecking at it to stimulate feeding (10). Begging varies from merely uttering a low call (score of 1) to jumping wildly up and down, flapping their wings, and calling loudly (score of 10). Thereafter we recorded feeding sequences whenever they could be observed from the onset. Data recorded included: date, time of day, nest number, parent (when known), chick that initiated feeding by running toward the parent or pecking at its bill (identified by band color), number of times each chick at the nest pecked at the parent's bill before the parent regurgitated food, chick that received the first food (by color band), and the number of times each chick pecked at food. If feeding sequences were initiated at more than one nest at a time, data were recorded from the nest where no previous feeding data had been recorded that day.

At the start of each observation period we noted a walking score [from 1 = lowest to 10 = highest, see Burger (11) for details] and noted the number of times a chick stumbled or fell when walking over a 1 m distance. The first chick to move was observed, followed by the second, and so on until all chicks were observed moving. During the weighing at 9 days of age we also placed the chicks on their backs to measure the time required to right themselves.

On 9 June it rained heavily on and off all day, and we recorded the time it took each chick to get under a parent for brooding at the onset of heavy downpours. Chicks that remain out in the open are potentially exposed to cold stress (14). Two additional field assistants participated in these observations.

Parental behavior was observed mainly with respect to feeding, one of the most important aspects of parental investment. During the chick feeding sequences described above we also noted which parent was feeding the chick. Male herring gulls are significantly larger than females, and the sexes can be distinguished in the field by sight when they are together (8,9). We expected that the parents would feed the chicks by regurgitating food at or near the nest, as is usually the case (9). By the 3rd day postinjection, it was apparent that the parents at some nests were dividing up the chicks for feeding. That is, the returning parent would call and initiate feeding, and the chicks would rush to it, begging loudly and pecking at the parent's bill. This would stimulate regurgitation, and the chicks began to feed. However, at some nests one chick begged less vigorously (had a lower begging score). At these nests the second parent often walked a short distance from the nest and gave a Long Call or Mew call to draw the chick that was not feeding to it. We defined this behavior as divided feeding. That is, both parents were feeding the chicks at the same time, but at two locations such that the more vigorous chick did not monopolize the food.

These observations were unexpected, and we designed the following protocol to study this parental investment behavior. We hypothesized that parents would engage in divided feeding if they had chicks with great weight disparity, and that divided feeding might enhance survival by preventing starvation. On day 3 postinjection JB observed behavior to determine which parents engaged in divided feeding, dividing the experimental pairs into divided and nondivided feeders. On days 4–7 and days 9–14 postinjection JB recorded the feeding behavior of all experimental pairs in the two categories (divided or nondivided) and of all control pairs. At the end of the observation period on day 7 and 14 postinjection, we weighed all chicks to determine any weight differences. Feeding behavior recorded for each bout included whether only one parent was present (thus only one could feed); and if both parents were present, whether there was divided or nondivided feeding.

General Health

We weighed the chicks on ony 3 days (9, 16, and 40 days of age) to reduce the effects of the investigators on their subsequent behavior and to reduce the chances that the chicks, particularly the lead-injected ones, would get lost during these disturbances. Our previous work in the laboratory indicated that lead-injected chicks exhibit delayed parental recognition (17), and, thus, might have more difficulty finding their parents following a disturbance.

Blood was collected at 40 days to facilitate comparisons with control birds in the wild (15,22).

Statistical Analysis

Statistical tests used include multiple regression models procedures (46) to distinguish the variables contributing to feeding rates of chicks; and Contingency Table χ^2 and Kruskal–Wallis χ^2 tests to examine differences between groups (47).

We used multiple regression model procedures (46) to construct models explaining variations in the dependent variable food obtained (as measured by number of pecks at the food) as a function of the independent variables. Independent variables included time of day, study plot, sex of the feeding parent, chick initiating feeding, chick to eat first, peck rate of each chick, type (lead, control, 3rd), and feeding rate of each chick by type. The first three variables did not enter any of the models as significant variables. The procedure determines the r^2 for the first variable, and does not enter the second variable if it does not increase the r^2 significantly; thus, variables that vary colinearly are not entered in the model (46).

For the purposes of analysis, data are presented for experimental nests as lead-injected, control, and 3rd chick; and for control nests as R (for red band), G (for green band) and 3rd chick. The 3rd chick was always the 3rd chick to hatch, usually 1–3 days later; however, the lead and control (experimental nests) and the R and G (for control nests) were each composed of half chicks that were hatched first and half chicks that were hatched second (however, both hatched the same day).

RESULTS

Chick Behavior

Behavioral scores. Lead injected chicks performed less well on all behaviors including walking and begging scores, and number of falls per 1 m (Table 1). Similarly, they missed the parent's bill more often when begging for food compared to their siblings. During the recurrent heavy rain showers on June 9, the lead-injected chicks took nearly a minute before they sought cover under their parents whereas their siblings were brooded within 3 s (Table 1). At 9 days of age (7 days postinjection) we were able to measure the time required to right themselves when placed on their backs; and lead-injected chicks took significantly longer than controls.

Feeding sequences. In the above observations we examined begging behavior once the chicks were begging. We also examined feeding sequences for experimental nests (n = 20 nests, 402 observation) when both lead-injected and control chicks were begging from one parent (the other parent was not on the territory), and the 3rd chick may or may not have been

TABLE 1

BEHAVIOR OF LEAD-INJECTED AND CONTROL HERRING GULL CHICKS 1–14 DAYS POSTINJECTION IN EXPERIMENTAL NESTS OF HERRING GULLS

	Lead-Treated	Control Chicks	Wilcoxon χ^2 (p)
Number of chicks	20	28	
Number of falls in 1 m	0.9 ± 0.9	0.06 ± 0.3	203 (0.0001)
Walking score	7.7 ± 1.4	9.2 ± 0.8	95.4 (0.0001)
Begging score	7.5 ± 1.4	9.2 ± 0.9	119 (0.0001)
Number of misses	1.0 ± 0.9	0.1 ± 0.5	183 (0.0001)
Seconds to right*	2.1 ± 0.2	1.0 ± 0.02	33.7 (0.0001)
Time to seek parent in rain (s†)	65.5 ± 13.3	2.8 ± 1.0	18.0 (0.0001)

Mean ± SE, $df = 1$.
* At 9 days of age (= 7 days postinjection). All others are means for days 1–14.
† During heavy rain, at 5 days of age (= 3 days postinjection).

begging. The lead-injected chicks initiated feeding less often than their control siblings, and they were the first to obtain food on fewer occasions (Table 2). The 3rd chick initiated feeding more often than the lead chick, and obtained food first more often than the lead chick (Table 2). This pattern is contrary to results from the control nests where the R and G chicks equally initiated feeding sequences and equally obtained the first food: 3rd chicks did not initiate feeding and did not obtain the food first (Table 2).

Begging stimulation. As a measure of the relative strength of their begging as perceived by their parents, we also measured the number of pecks at the parent's bill required before the parent regurgitated (Table 2). The lead-injected chicks made significantly fewer pecks at their parent's bill than did the control chicks. Third chicks had intermediate levels of pecking, although because they were younger and smaller, their pecks were often less effective. In the control nests, there were no differences in pecking rates for R and G chicks, but 3rd chicks had lower pecking rates (Table 2).

As a measure of the competitive ability of chicks we measured the number of food items obtained when the chicks were being fed by only one parent (Table 2). Control chicks obtained the most food, followed by 3rd chicks, and then by the lead-injected chicks in the experimental nests. In the control nests, the R and G chicks obtained an equal number of items, but the 3rd chick obtained only half as many (as measured by pecking rates at the food, Table 2).

To some extent, initiating feeding by pecking at the parent's bill is an indication of desiring food. When control chicks initiated feeding, they obtained the first food a higher percentage of time than either lead-injected or 3rd chicks, although usually the chick initiating feeding more often obtained the food than the other chicks for experimental nests ($\chi^2(4) =$ $p < 0.01$, Table 3).

We also examined the number of pecks required to stimulate parents to regurgitate and the number of food items (or parts thereof) obtained as a function of which chick initiated the feeding sequence in the experimental nests. The chick initiating the sequence made more pecks, and obtained more food than the other chicks. However, both control and 3rd chicks obtained more food when they initiated feeding than did the lead chicks. Moreover, 3rd chicks obtained more food than the lead chicks except when the lead chick initiated feeding (Table 4).

We used GLM procedures to determine the factors contributing to how much food (as measured by number of pecks at the food) each chick obtained during feeding sequences at

TABLE 2

BEGGING AND FEEDING BEHAVIOR IN LEAD-INJECTED AND CONTROL HERRING GULL CHICKS AT EXPERIMENTAL NESTS (n = 20 NESTS, 402 OBSERVATIONS): AND RED AND GREEN (BOTH CONTROL) CHICKS AT CONTROL NESTS (n = 12 NESTS, 115 OBSERVATIONS)

	Percent of Times Initiate Feeding	Mean Number of Pecks Before Feeding	Percent of Times Fed First*	Mean Number of Items Obtained
Experimental Nests				
Control	48	2.20 ± 0.08	47	3.48 ± 0.09
Lead	18	0.93 ± 0.06	20	2.06 ± 0.09
3rd	34	1.62 ± 0.10	33	3.00 ± 0.14
χ^2 (p)	69.8 (0.0001)	104 (0.0001)	41.2 (0.0001)	36.9 (0.0001)
Control Nests				
R chick	50	3.31 ± 0.30	50	4.24 ± 0.27
G chick	50	3.43 ± 0.23	50	4.35 ± 0.31
3rd chick	0	1.67 ± 0.36	0	2.18 ± 0.29
χ^2 (p)	NS†	118 (0.0001)	NS†	48.6 (0.0001)

Observations equally divided among nests.
* Even if the chick did not initiate feeding.
† NS = Not significant, for R and G only.

TABLE 3

RELATIONSHIP BETWEEN INITIATING BEGGING AND OBTAINING THE FIRST FOOD IN EXPERIMENTAL NESTS OF HERRING GULLS

	Chick That Fed First		
Chick Initiating Begging	Control	Lead	3rd Chick
Control	218 (92%)	15 (6%)	3 (2%)
Lead	24 (28%)	57 (67%)	4 (5%)
3rd Chick	8 (22%)	4 (10%)	25 (68%)

Shown are number (percents).

experimental nests (Table 5). For all three types of chicks, which chick initiated feeding entered the models, and for the lead and control chicks, the identity of the first chick to eat and the initial pecking rate at the parent's bill were significant contributors to explaining variations in amount of food obtained. For 3rd chicks, the significant contributors were which chick initiated feeding and its own pecking rate (Table 5).

Chick Growth and Weight

There were no significant differences in the weights of the lead-injected and saline-injected control chicks at the initiation of the experiment (Table 6). By 9 days of age the weight difference approached significance ($p < 0.08$), and by 16 days of age there was a significant difference (Table 6). At 40 days of age, however, there was no longer a significant difference in weight between the lead-injected and control chicks.

Parental Behavior

For all nests, both experimentals and controls, at least one parent was present all of the time when nests were being observed several hours each day, until the chicks were at least 21 days old. In all nests parents remained in attendance some of the time until the chicks were 40 days of age, and parents still actively dive-bombed intruders.

When only one parent was present on the territory and that parent commenced regurgitation to feed the chicks, and when the chicks were begging, there appeared to be no parental selection of which chick obtained the food at the experimental nests. However, when only one parent was in attendance at experimental nests, and only one chick was begging (chick ages 3–8 days), the parent held the food in its bill (rather than dropping it) for the lead-injected chick (88%, $n = 36$) more often than for control chicks (23%, $n = 78$, $\chi^2 = 43.3$, $p < 0.0001$).

Feeding sequences could be performed by one parent when it was the only parent present on territory, by one parent when the other parent was on territory but not engaged in feeding (nondivided), and by both parents who were separated by at least 0.5 m (divided feeding). On day 3 postinjection we assigned each experimental nest to a type (divided or nondivided feeders) based on whether more than 10% of the feedings involved divided feeding. This was arbitrary, but, in fact, the parents at most nests seemed to either engage in all divided feeding or none. Thereafter we recorded all feeding sequences as solitary (one parent present), divided or nondivided (both parents present), and examined them by nest type.

There was a significant difference in the method of parental feeding as a function of the feeding category of the pair when the chicks were 4–7 days postinjection [Contingency Table $\chi^2(4) = 166$, $n = 902$ feedings, $p < 0.001$], and 9–12 days postinjection [$\chi^2(4) = 73.6$, $n = 606$ feedings, $p < 0.0001$, Fig. 1). At the end of the 7th day postinjection (9 days of age) there was a greater difference in weight between the lead-injected and control chicks (mean $= 48 \pm 10$ g) in the nests of parents that engaged in divided feedings compared to those that were not categorized as divided feeders (mean $= 16 \pm 2.7$ g, Fig. 2). Moreover, for the divided feeders, the difference in weight between the lead-injected and control chicks increased as the weight of the heaviest chick increased (Fig. 2).

TABLE 4

FEEDING BEHAVIOR AS A FUNCTION OF THE CHICK INITIATING FEEDING FOR CHICKS IN THE EXPERIMENTAL HERRING GULL NESTS

	Chick Initiating Feeding		
	Control	Lead	3rd Chick
Number of pecks before feeding by			
Control	2.75 ± 0.09	0.85 ± 0.12	1.60 ± 0.23
Lead	0.46 ± 0.05	2.24 ± 0.14	0.81 ± 0.18
3rd Chick	1.32 ± 0.12	1.55 ± 0.28	2.60 ± 0.15
Number of feeds by			
Control	4.19 ± 0.10	2.34 ± 0.19	3.14 ± 0.28
Lead	1.85 ± 0.12	3.19 ± 0.19	1.54 ± 0.31
3rd Chick	2.69 ± 0.20	2.46 ± 0.30	4.03 ± 0.20

Sample sizes shown on Table 3.

TABLE 5

MODELS (PROC GLM) EXPLAINING VARIATIONS IN FOOD OBTAINED (NUMBER OF PECKS AT FOOD) FOR CONTROL, LEAD AND 3RD CHICKS IN EXPERIMENTAL NESTS OF HERRING GULLS

	Control	Lead	3rd Chick
Model			
F	5.64	6.29	4.73
r^2	0.52	0.52	0.52
p	0.0001	0.0001	0.0001
df	3,399	5,397	2,400
Factors entering the model (*F*,*p*)			
Chick initiating feeding	23.8 (0.0001)	15.3 (0.0001)	11.1 (0.0001)
Chick to eat first	13.7 (0.0001)	8.7 (0.0003)	NS
Peck rate of lead-chick	NS	18.7 (0.0001)	NS
Peck rate of control chick	16.4 (0.0001)	7.7 (0.006)	NS
Peck rate of 3rd chick	NS	NS	48.9 (0.0001)
Sex of parent feeding	NS	NS	NS
Nest number	NS	4.4 (0.0001)	NS

Given are *F* values (probability levels) for factors entering the best model.

Fledging Success

Overall fledging success was significantly lower for lead-injected compared to control chicks (Table 6). Death rates were higher for the lead-injected chicks for the pairs that were categorized as divided feeders at ages 4–7 postinjection (6 of 20 lead-injected chicks died compared to 2 of 20): however, none of the chicks in the nests that were divided feeders died from 9–14 days postinjection, whereas 2 of 18 chicks died in the nondivided category from 9–14 days postinjection [$\chi^2(2) = 4.5, p < 0.05$]. Thus, it appears that parents engaged in divided feeding when they perceived a weight difference (or some other difference) between their chicks within days after injection, but they still lost some of the lead-injected chicks: whereas parents that did not perceive a difference did not engage in divided feeding, and lost more of their chicks at a later age.

We also examined survival for the entire period, until 40 days of age, and parents that engaged in divided feeding fledged more chicks than those that did not engage in divided feeding [$\chi^2(1) = 8.28, p < 0.01$]. This difference was due to survival of the lead-injected chicks: more lead chicks survived overall in nests with divided feeding than in nests without divided feeding [$\chi^2(1) = 8.66, p < 0.01$].

DISCUSSION

Overall these results indicate that there were lead-induced differences in behavior in the field, there were similar lead-induced deficits in the field and laboratory, siblings competed for food, and parents compensated for the behavioral deficits of their chicks. Each aspect will be discussed below.

Lead-Induced Differences in Chick Behavior

In this experiment there were several differences in behavior as a function of lead treatment including: a) initial growth, b) walking ability, c) righting response, d) seeking cover (from inclement weather), e) begging behavior, and f) feeding behavior. These were described in more detail in Burger and Gochfeld (19). Moreover, there was a difference in fledging rate between lead-injected and control chicks. Thus, the deficits in behavior, or other unrecorded behaviors, resulted in lowered survival rates. The differences in survival were not due to immediate toxic effects because no chicks died within 4 days of injection.

All of the behavioral deficits observed relate directly or indirectly to survival of gull chicks in the wild. Initial growth

TABLE 6

WEIGHT (MEAN ± SE GR) AND WEIGHT GAIN OF HERRING GULL CHICKS IN EXPERIMENTAL NEST

	Experimental Chicks	Control Chicks	Wilcoxon χ^2 (*p*)
Initial Weight	88.3 ± 7.4	82.4 ± 7.2	1.3 (NS)
Weight at 9 days	95.8 ± 7.1	118.8 ± 8.5	3.0 (0.08)
Weight gain (age 2–9 days)	7.4 ± 7.8	36.3 ± 3.1	14.7 (0.0001)
Weight at 16 days	131.3 ± 14.3	188.9 ± 17.7	6.6 (0.01)
Weight gain (age 9–16 days)	42.1 ± 13.4	82.3 ± 11.2	8.7 (0.003)
Weight at 40 days	825 ± 62	890 ± 21	4.0 (0.13)
Blood lead at 40 days (μg/dl)	25.8 ± 4.7	10.0 ± 0.5	12.6 (0.001)
Fledging rate* (Total No. of chicks in sample)	55% (20)	89% (28)	7.4 (0.05)

Given are mean ± SE.
* Chicks fledge, or leave the nest, at about 45 days of age.

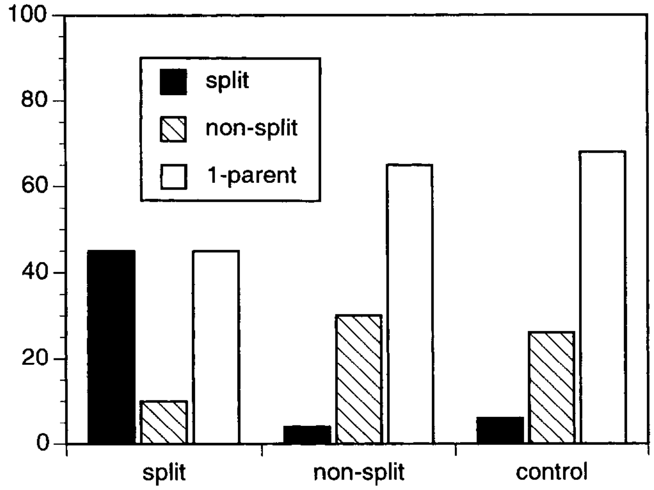

FIG. 1. Parental feeding behavior as a function of nest type for herring gull nests. Percent of feedings that were split (both parents present and both fed, black bar), both parents present but only one fed (hatched), or only one parent was present and fed (open bar).

is critical because smaller chicks are at a competitive disadvantage with their larger siblings when seeking food from their parents (34,36). Indeed, lead-injected herring gull chicks in this experiment obtained less food than their siblings, when directly competing with them. They even obtained less food than their 3rd chick siblings, except when they initiated feeding sequences.

Walking ability and righting response are critical for predator avoidance and in reaching their returning parent in time to obtain some of the food. When aerial predators, such as other gulls or hawks, enter the colony chicks that can quickly reach cover under their parents, vegetation or debris can often avoid predation (6). Moreover, chicks that do not reach their parents as soon as their siblings, when they first return to the territory with food, often obtain less food (16).

The ability to seek cover from inclement weather is critical because chicks are vulnerable to both heat and cold stress (7). Extreme heat stress (2,28,33), wind (32), and heavy rain and fog (7,16) can cause mortality. Thus, the ability to quickly find cover is important for survival in the wild.

Begging and feeding behavior are clearly important for growth and survival. Chicks that are less able to compete with siblings obtain less food, and could starve (34,49). However, begging behavior is also important because herring gull young obtain all of their food resources from their parents, and chicks stimulate the parents to provision them by the intensity of their begging behavior (48). Thus, if all the chicks in a brood were impaired by lead, as might normally occur because chicks are being fed the same foods, the combined lower begging responses might decrease the total stimulus to parents to leave in search of food, but this requires field testing.

Lead-injected chicks gave fewer pecks at their parent's bill when begging compared to control or 3rd chicks. Thus, even though the lead chicks were older than 3rd chicks, they were less vigorous at begging. When they did initiate begging, however, they pecked at their parent's bill more often than their siblings. Thus, the overall picture that emerges is that control and 3rd chicks in experimental nests beg more vigorously and

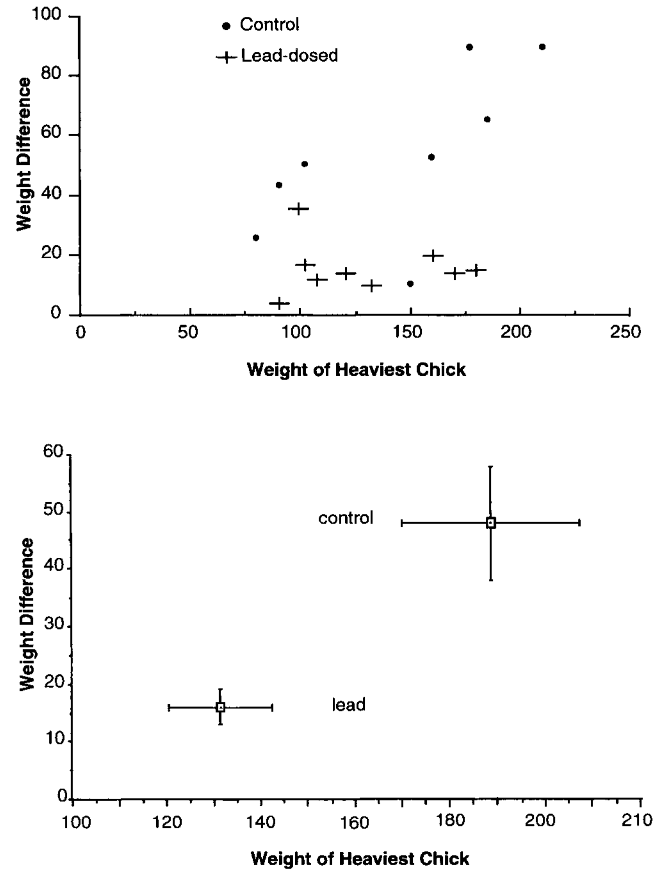

FIG. 2. Top: weight difference (g) between the lead and control chicks in experimental nests as a function of the weight of the heaviest chick (always the control chick) at 16 days of age. Bottom: mean and range for the weight (g) of the heaviest chick plotted against the weight difference for control chicks (top) and for lead gull chicks (bottom) at 16 days of age.

obtain more food than lead chicks (see sibling competition below).

One might argue that the experimental creation of only one chick in each brood with lead exposure is artificial and would never occur in the wild. Although this may be true generally, differences in lead levels in chicks could occur because pollutant levels can differ as a function of egg-laying order [levels are higher in the first egg, (24)], and parents may feed different chicks different foods. Some chicks prefer to eat one kind of food over another, and these diet preferences can affect their exposure. Moreover, there is some adoption in gulls (23), and, thus, chicks with different levels of pollutants obtained either from the egg or from parental provisioning before adoption, can end up together in the same nest. Thus, for a variety of reasons, chicks with different pollutant loads can end up in the same brood.

Comparison of Field and Laboratory Lead Effects

Unlike most toxicological studies, these experiments were conducted on birds in the wild that were able to engage in all of their normal behaviors; parents had normal interactions with their chicks and neighbors, parents flew several kilometers away to forage for food, parents brought back normal foods to feed the chicks, and parents engaged in normal feeding, nest, and chick defense, and interactions with neighbors. Likewise, the chicks were exposed to natural forces such as predation, exposure to the elements, and competition with their siblings for food and protection. Furthermore, the lead levels that we injected them with were similar to those young herring gulls can encounter in the wild (18,21,22).

Rarely have the effects of lead (or any other pollutant) been examined experimentally in truly wild, unrestrained birds. This is due to the obvious difficulties of: a) having sufficient sample sizes of breeding birds in close proximity that can be easily observed, b) controlling other causes of mortality to allow completion of the experiment, and c) having sufficient laboratory data on dose–response effects to determine appropriate sublethal doses for experimentation. The method that comes the closest involves restraining birds to limited spaces (either in large, covered flight pens or by pinioning birds so they cannot fly away). For example, Heinz (31) examined the effect of methymercury on survival and reproduction of three generations of ducks, and reported intergenerational effects.

Before initiating the field experimentation we conducted extensive laboratory experiments on the effects of lead on terns (*Sterna hirundo*) and herring gulls from 1983 through 1993 (11–13,17). We used these experiments, in addition to data on known levels of lead in feathers of gulls from the Captree colony (18), to determine the dose to be used in the field experiments. Effects assessment, environmental impact assessment, and risk assessment often require extrapolation from laboratory results to predict future effects on individuals and populations in the wild (44), and it is important to examine in nature doses that mimic actual exposure. Blood lead levels of the gulls at 40 days of age were 25.8 ± 4.7 μg/dl (22). For comparison, the control chicks averaged 10.0 ± 0.5 μg/dl for birds in the wild. Even in a few short weeks chicks in the wild encounter lead.

In this section we compare field and laboratory effects using the same dose. Because of constraints on our ability to handle chicks in the wild (and our ability to make observations from afar on unrestrained and uncaged gulls in the laboratory), different tests were often used to examine the same behavior. We handled the field birds as little as possible to avoid effects due to human disturbance.

Some tests, however, were performed with the same exact methodology: for both laboratory (20) and field experiments, lead-injected chicks took significantly longer to right themselves than did controls. This behavior can be important in the wild because chicks can stumble and fall down dunes or other natural inclines, and are vulnerable to predators and aggressive neighbors until they are back on their feet and able to escape. Similarly, lead-injected chicks stumbled more when they walked than did control chicks in both the laboratory experiments and in the field.

In the laboratory, control chicks perform better on thermoregulation tests: they are able to reach shade and remain in the shade for longer than lead-injected chicks (11). Field chicks were not tested on a thermoregulation apparatus, but control chicks sought cover under their parents significantly quicker when exposed to sudden downpours than did lead-injected chicks. Heavy downpours and continuous rains pose a particular threat to young chicks, and prolonged rain can cause chick mortality (7,14).

Begging is one of the most important behaviors chicks can perform because it stimulates parents to regurgitate or to find additional food (10). In the laboratory, begging intensity can be decreased or increased in lead-injected chicks, depending upon species and food type (11,13), perhaps because chicks are underweight and not receiving enough food. In the field, however, lead-injected herring gull chicks had significantly lower begging scores, made fewer pecks at their parent's bill to stimulate regurgitation, and missed the bill more often when they were pecking at it than did control chicks. Thus, in the field, lead chicks seem to be at a greater disadvantage than predicted by the laboratory results. This may have been a function of the method of testing. In the laboratory, begging scores were determined when each chick was offered food alone, whereas in the field chicks were observed together with other siblings as they all begged from parents. Thus, lead chicks were less able to compete with siblings or were overshadowed by them.

In the laboratory, lead-injected chicks did not obtain enough food when they competed with their control cage mates (11,17), and so lead-injected chicks were fed after their cage mates ceased eating. In the wild, the lead-injected chicks also were at a competitive disadvantage when eating with their control and 3rd chick siblings. That is, in feeding sequences with their siblings, lead-injected chicks obtained the first food less often, and were able to peck at food (and eat it) less often than their siblings.

We tested individual recognition in the laboratory (17), but were unable to test it in the field. In the laboratory, lead delays individual recognition by several days. Presumably chicks that are able to wander about before recognition develops might encounter hostile neighbors or predators (4,9,25). In this experiment we observed two lead-injected herring gull chicks being killed and eaten by neighboring great black-backed gulls (*Larus marinus*) when they wandered far from their own nests. Their siblings remained near the nest, and ultimately fledged. This may have occurred because the chicks did not recognize their parents, but this requires field testing.

In the laboratory lead retards growth in weight and bill, tarsus, and wing length, and most of these deficits persisted until the chicks were 40 days of age (13). In the field, weight differences were apparent ($p = 0.08$) at 9 days of age, whereas there were significant weight differences in the laboratory by 8 days of age (13). The weight differences between lead and control chicks widened in the field gulls by 16 days of age, but disappeared by 40 days of age, just before fledging. We partly attribute this difference in fledging weights between laboratory and field results to parental behavior (see below).

Overall, the results from the field generally corroborate results from the laboratory for exact or similar tests, indicating behavioral deficits as a function of lead exposure. Some of the deficits could lead to increased predation because chicks did not walk as well, and could right themselves less quickly. Some of the deficits (in sibling competition, begging, and feeding) could lead to parental neglect and chick starvation.

Sibling Competition

In many species of birds the parents begin incubation before the clutch is complete, and this results in asynchronous hatching. The last hatched chick is at a disadvantage because when it hatches it is smaller and younger than its siblings, and is at a competitive disadvantage (29,34,36,37,40). Indeed, one explanation for asynchronous hatching is that it provides a mechanism for brood reduction when food is limiting, and by placing a clear disadvantage on one chick (the last hatched), it reduces unnecessary competition between siblings by making the outcome obvious.

In the case of asynchronous hatching, the difference in offspring quality is due to age and size, and not to the inherent quality of the offspring. In this experiment we examined sibling competition where the differential quality of the offspring was a function of lead exposure, and half of the chicks so exposed were first hatched and half were second hatched. In the control nests, where half of the R and G chicks were first hatched, and half were second hatched: there were no competitive differences in begging and feeding between the R and G chicks, but the 3rd hatched chick was at a competitive disadvantage and obtained less food. This is what usually happens in asynchronous nests: the last hatched chick is at a competitive disadvantage and often dies (26).

Results from the experimental nests, however, indicated that the lead-exposed chicks were clearly impaired with respect to ability to initiate feeding, begging intensity and number of pecks at the bill, access to the first food, and number of food items obtained. Instead of the 3rd chick being at a competitive disadvantage in the experimental nests, the lead-chick was. However, whichever chick initiated feeding by pecking at its parent's bill usually obtained the most food. Thus, one strategy open to the lead chicks (and presumably to any behaviorally impaired chick) is to initiate a feeding sequence soon after their siblings are satiated from a previous feeding. If parents still have some food available for regurgitation, the disadvantaged chick could stimulate feeding at a time when its siblings are less interested in eating.

Parental Investment and Parental Compensation

In this experiment the lead-injected chicks experienced slower growth and behavioral deficits (less effective begging and a competitive disadvantage in obtaining food). Within 2–3 days of injection, parents seemed to assess this problem, and responded accordingly. That is, parents whose chicks experienced a great difference in weight began to divide up the chicks for feeding. This reduced the competition between the chicks in a brood because smaller, lighter, less vociferous chicks were not required to compete for food with larger siblings during all of the feedings. Moreover, the parents whose chicks experienced less of a discrepancy in weight engaged in a significantly lower percentage of divided feedings than parents with a large discrepancy in chick weights, and their rate of divided feeding was similar to that in control nests (with no lead-injected chicks). Overall, survival rates were lower for lead than control chicks; but survival rates were higher for lead chicks whose parents engaged in divided feedings than for lead chicks whose parents did not.

These results are of interest because they indicate: a) in nature parents have a behavioral method of countering the initial effects of lead (lower growth, decreased begging, and less vigorous feeding by chicks, and possibly delayed parental recognition); b) parents can perceive a difference in behavior and/or growth of their chicks and respond accordingly; and c) contrary to much of the current theory on parent–offspring conflict, parent herring gulls expend extra effort to ensure that the smaller, lead-impaired chicks obtain food.

Genetic conflicts of interest can exist in any society, and are particularly evident between offspring and parents (27,50,51). However, Burger (8) argued that such conflicts sometimes occur over when to give the care, and not whether to give the care, and that equitability in parental investment results in higher reproductive success than unequal care (10).

In this study with herring gulls, the parents chose not to abort their investment in the suboptimal chick when there was a large size difference and behavioral deficits between the young. The differences were sufficient to result in the larger chicks monopolizing much of the food initially. This competitive difference resulted in a weight disparity between the lead and control chicks. Parents with a large difference in weight between their chicks engaged in divided feeding, where both parents fed chicks at the same time but in separate places. This eliminated sibling competition because the disadvantaged chick was fed alone. In this case, the parents did not merely feed the chicks, passively allowing the best competitor to obtain the food, but actively worked to ensure that the weaker chick obtained food.

Parents without a large weight difference between their chicks engaged in a significantly lower rate of divided feedings (equal to that in control nests), suggesting that parents are able to perceive a difference in quality of their young. It is not clear whether parents were responding to a difference in weight, size, or behavioral deficits in begging, feeding and locomotion.

The division of a brood for feeding of prefledging chicks has not generally been noted in the literature [but see Horsfall (32) for Coot], perhaps because it is sporadic and occurs with a low frequency. Brood division does occur, however, after fledging in a number of altricial birds (29,30). Moreover, the association of increased rates of divided feeding with suboptimal chicks might not be obvious. In this study, only 4–6% of the feedings in control nests were divided feedings. This makes divided feeding relatively rare in any given nest, and divided feeding has not been the focus of an in-depth study. Nonetheless, the rare presence of divided feeding does provide a basis for a behavioral switch to a much higher rate of divided feeding when one offspring is behaviorally impaired (or simply smaller or lighter).

One remaining question is why the parents chose to provide parental care to these suboptimal chicks. Parent–young conflict theory predicts that the parents should simply dispense care and let the offspring compete (with suboptimal young eventually starving). Partly, the lead-injected chicks may have been giving contradictory stimuli: their begging behavior was aggressive when their siblings were not the first to initiate feeding, although they missed their parent's bill more often and were unable to compete for food as effectively as their siblings once the parents began to feed. Secondly, food did not seem to be a problem in 1993 at Captree, and both parents at most nests spent a great deal of time on the territory loafing and resting (indicating they were required to devote little time to foraging). Perhaps in good food years the cost to parents of extra parental care is relatively low.

Nonetheless, the overall effect of the intensive care involved in divided feeding resulted in increased survival for chicks that reached 2 weeks of age, and a lack of weight difference between lead-injected and control chicks at fledging. This later finding was remarkable because in the laboratory we were unable to eliminate a lead-induced weight difference by 40 days of age despite individual feedings to all chicks. In the laboratory the technicians fed every chick until it no longer wanted to eat. Thus, these experiments indicate that parents can perceive a difference in the quality of their offspring, perform additional parental care in the form of divided feedings, and manage to decrease the death rate and increase the growth rate of their lead-impaired offspring such that they were not significantly underweight at fledging. Thus the parents compensated for the lead impairment by behavioral mechanisms.

ACKNOWLEDGEMENTS

We thank N. Morganstein and M. Bixby for field and laboratory assistance, C. Safina and M. Lee for logistical support, Alex Gochfeld for translation of Russian articles, and D. Mock, C, Safina, K. Reuhl, and H. Lowndes for helpful comments on the research and/or manuscript. The New York State Department of Environmental Conservation, the U. S. Fish and Wildlife Service, and the Long Island State Park Commission provided permits to work with herring gulls and to collect specimens where necessary. This research was funded by NIEHS Grants ES 05022 and ES 05955, and the Environmental and Occupational Health Sciences Institute.

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