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## GAMMA IRRADIATION OF TREE SWALLOW EMBRYOS AND SUBSEQUENT GROWTH AND SURVIVAL<sup>1</sup>

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**Abstract.** Tree Swallow (*Tachycineta bicolor*) eggs from 35 nests, 7 to 8 days into incubation, were acutely exposed to gamma-radiation doses of about 0.4, 0.8, 1.6 or 3.2 Gy in the laboratory. The naturally incubated eggs were hatched in the laboratory and the young returned to the nests for raising by parents. Transport controls were treated identically, but not irradiated; box controls were left undisturbed in the nests. The overall mean hatching and fledging successes were 92.8% and 71.8%, respectively, and were unaffected by radiation exposure. Nestlings died from several causes including predation and harsh weather. Observed statistics and fitted parameters from the Richards model both indicated depressed growth in the 1.6-Gy and 3.2-Gy nestlings. Radiation exposure increased incubation time and depressed body mass and foot and primary-feather lengths at fledging. Box controls had shorter incubation times and greater hatching body masses than transport controls, suggesting experimental stress factors other than radiation exposure. Data from a few nests showed that chronic doses of about 1.0 Gy·d<sup>-1</sup> reduces hatching, but not fledging, success. It also depresses growth far more severely than a 3.2-Gy acute dose. Since Tree Swallow embryos appear to be less sensitive to external gamma-radiation exposure than man, existing protective measures for man should be satisfactory for birds.

**Key words:** *Acute stress; breeding success; chronic stress; environmental protection; gamma-radiation exposure; radiation biology; Richards growth model; Tree Swallow.*

### INTRODUCTION

In spite of the high interest in nuclear issues surrounding power generation, medicine, food preservation, tracers, and defense, reliable information on radiation effects on wild birds is very limited (Odum 1971, Mellinger and Schultz 1975, Whicker and Schultz 1982). This is unfortunate because future decisions concerning these issues should be based on sound data. Birds seem to be exceptionally sensitive to man-made environmental stresses, particularly during early development (Fendley and Brisbin 1977, Gilbertson and Fox 1977, NRC 1979, Helander et al. 1982). Thus, they could represent one of the most sensitive links in the environment and could assume the role of biological indicators (Norstrom et al. 1978, Halford et al. 1981, Kendall 1982).

We have previously studied the effects of gamma radiation on nestling Tree Swallows (*Tachycineta bicolor*) and House Wrens (*Troglodytes aedon*; Zach and Mayoh 1984, 1986).

The results showed that nestling birds are relatively insensitive to radiation exposure in terms of mortality, but not in terms of growth. Developing embryos, rather than rapidly growing nestlings, however, may be the most sensitive stage (Wetherbee 1966).

Here we present a field experiment involving acute gamma irradiation of Tree Swallow eggs during incubation. The objectives of the study were to determine the effects of radiation on hatching, growth and fledging. Also presented are data on chronic irradiation of Tree Swallow eggs and nestlings, and a discussion of basic radiobiological and environmental protection principles, as related to birds.

### METHODS

#### STUDY AREA AND GENERAL PROCEDURES

The study was carried out in 1984 in an established Tree Swallow colony in a mixed-forest area with interspersed meadows, at the Whiteshell Nuclear Research Establishment near Pinawa, Manitoba, Canada (Zach and Mayoh 1982a).

Thirty-five nests were checked daily from nest building on. About half-way into incu-

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bation, all or most of the eggs from each nest were temporarily taken into the laboratory where all but one were irradiated. During this period of about 1 hr, dummy eggs were placed into the nests to prevent desertion. Dummy eggs were boiled, satin-lacquered Tree Swallow eggs marked with a small green dot. Shortly before hatching, the experimental eggs were taken to the laboratory for hatching so that the young could be traced to their eggs. During this period dummy eggs were again substituted; they were later replaced by the appropriate hatchlings.

Eggs and young were transported in an insulated box with a battery-powered heater, to maintain their temperature around 35°C. Hatchlings were marked with colored thread tied around the lower leg, which was later replaced by an aluminum leg band. Growth and survival were recorded daily until fledging.

#### EXPERIMENTAL DESIGN

We took five eggs from each nest to the laboratory and exposed four of them to gamma-radiation doses of about 0.4, 0.8, 1.6 and 3.2 Gy (1 Gy = 100 rad). One of the eggs was left unirradiated as a transport control. In clutches with six eggs, one egg was left undisturbed in the nest to serve as a box control. All eggs were assigned to treatments randomly and were color-coded for identification. The irradiated eggs and the transport controls formed a randomized block experiment (Snedecor and Cochran 1967) with five treatments to control for pronounced growth differences between broods (Zach and Mayoh 1982b). Box controls were excluded from this design because about half of the nests had only five eggs. Transport and box controls were compared separately to evaluate experimental effects other than radiation exposure.

#### IRRADIATION PROCEDURES

Eggs were irradiated on incubation days 7 to 8, assuming that incubation started on the day before the last egg was laid (Zach and Mayoh 1982b). At this stage of incubation, bird embryos are likely very sensitive to radiation exposure (Muller and Moreng 1966, Wendt 1981). A Gammacell 220 irradiator (Atomic Energy of Canada Limited) was used, with a dose rate of 0.06 Gy·s<sup>-1</sup> absorbed in air. The eggs were placed into a container and mechanically lowered into a ring-shaped <sup>60</sup>Co source for uniform exposure. The actual mean doses for the four irradiation treatments were ( $\bar{x} \pm \text{SE}$ ) 0.44 ± 0.01, 0.87 ± 0.01, 1.65 ± 0.03 and 3.43 ± 0.07 Gy, as determined by lithium fluoride thermoluminescent dosimeters (Zach and Mayoh 1982a). Our irradiator

did not allow us to achieve the exact target doses of 0.4, 0.8, 1.6 and 3.2 Gy.

#### HATCHING PROCEDURES

Irradiation and transport-control eggs were hatched in an incubator, following Mayoh and Zach (1985). Briefly, 2 to 3 days before the expected date of hatching, eggs were placed into individual styrofoam compartments in an incubator maintained at about 35°C with a relative humidity of about 60%. Eggs were turned several times daily. Hatching was deemed complete when a young had freed itself from at least one of the eggshell halves. Young were returned to the appropriate nests within 16 hr of hatching. Eggs were weighed on a laboratory balance to the nearest 0.001 g before putting them into the incubator. Young were also weighed immediately following hatching to determine the hatching body mass. Box controls were allowed to hatch naturally in their nests, and the first weight taken corresponds to the hatching body mass.

#### GROWTH DATA

The body mass and primary-feather and foot lengths of each young were measured daily. Nestlings were weighed in a small plastic bag with a spring scale to the nearest 0.1 g. The other measurements were made to the nearest 0.5 mm with a ruler. We measured primary feather No. 10 from the base to the tip of the pin or vane (Zach and Mayoh 1982b). The foot was measured flat from the posterior edge of the heel to the base of the claw of the middle toe.

#### OBSERVED GROWTH STATISTICS

We used several observed growth statistics for assessing radiation effects. The hatching body mass is the first value recorded at age 1, the hatching day; the body-mass asymptote is the highest measured value; fledging body mass is the last recorded value; and recession body-mass loss is the drop in mass from the asymptote to fledging (Zach and Mayoh 1982b). The incubation time extended from the start of incubation to the hatching day; the nestling time extended from the hatching day to the fledging day; the time to body-mass asymptote is the age at highest body mass; and the recession time is the period of body-mass loss from the asymptote to fledging. The time to primary-feather emergence is the age at primary-feather appearance, and the emergence primary-feather length and the fledging primary-feather length are the first and last values recorded. Finally, the fledging foot length is the last value measured just before fledging.

TABLE 1. Percentage of hatched, unhatched and missing eggs.

| Treatment         | <i>n</i> | Hatched | Un-hatched <sup>a</sup> | Missing <sup>b</sup> |
|-------------------|----------|---------|-------------------------|----------------------|
| Transport control | 35       | 91.4    | 5.7                     | 2.9                  |
| 0.4 Gy            | 35       | 94.3    | 5.7                     |                      |
| 0.8 Gy            | 35       | 100.0   |                         |                      |
| 1.6 Gy            | 35       | 91.4    | 5.7                     | 2.9                  |
| 3.2 Gy            | 35       | 97.1    | 2.9                     |                      |
| Box control       | 17       | 82.3    | 11.8                    | 5.9                  |

<sup>a</sup> Infertile eggs or dead embryos.

<sup>b</sup> Removal by a parent or breakage.

#### CURVE-FITTING AND GROWTH-MODEL PARAMETERS

We used the flexible Richards growth model (Richards 1959) integrated with respect to time (Causton 1969),  $M(t) = A(1.0 \pm e^{-Kt})^{-1/n}$ , where  $M(t)$  = mass (g) or length (mm) at time  $t$  (days),  $A$  = asymptotic mass (g) or length (mm),  $c$  = constant of integration,  $K$  = growth-rate constant ( $d^{-1}$ ) and  $n$  = shape parameter. The more conventional sigmoid von Bertalanffy, Gompertz and logistic models are special cases of the Richards model (Zach et al. 1984). The model was fitted to the growth data of individual nestlings using a least-squares method (Liner et al. 1985, Zach et al. 1984). White and Brisbin (1980) introduced an alternative method for fitting the Richards model using a process error model. However, since their method assumes that measurements such as body mass can be taken without error, it will likely be of limited use in field studies. We used the growth-model parameters  $A$ ,  $K$  and  $n$  for assessing radiation effects.

Because Tree Swallows have pronounced body-mass recession before fledging (Zach and Mayoh 1982b), we used data up to and including the body-mass asymptote for curve fitting. For primary-feather length, all the data were used because growth is incomplete at fledging (Zach and Mayoh 1982b). This can lead to problems in curve fitting and the results may, therefore, be only approximate. Foot-length growth is very rapid and we used data up to and including 10 days of age, which in all cases included the fledging foot length. Inclusion of values beyond ten days would have de-emphasized the actual growth of foot length. The numbers of observations used for fitting to body mass and primary-feather length ranged from 11 to 20 and from 13 to 17, respectively. For foot length, 10 observations were used throughout.

#### STATISTICAL ANALYSIS

Analysis of the randomized block experiment was complicated by egg and nestling losses. A few eggs disappeared or failed to hatch. Amer-

TABLE 2. Percentage of fledged, preyed and dead nestlings.

| Treatment         | <i>n</i> | Fledged | Preyed <sup>a</sup> | Dead <sup>b</sup> |
|-------------------|----------|---------|---------------------|-------------------|
| Transport control | 32       | 71.9    | 12.5                | 15.6              |
| 0.4 Gy            | 33       | 66.7    | 15.1                | 18.2              |
| 0.8 Gy            | 35       | 74.3    | 8.6                 | 17.1              |
| 1.6 Gy            | 32       | 71.9    | 12.5                | 15.6              |
| 3.2 Gy            | 34       | 67.6    | 14.7                | 17.7              |
| Box control       | 14       | 78.6    | 14.3                | 7.1               |

<sup>a</sup> By kestrels and a few small dead young possibly removed by a parent.

<sup>b</sup> Due to exposure, starvation, abandonment and possibly radiation exposure.

ican Kestrel (*Falco sparverius*) predation, harsh weather conditions and, perhaps, parasitic fly larvae (*Protocalliphora* sp.) took their toll of nestlings. Depending on the age of these young, their data could still be used for various comparisons. In a few cases, missing values were estimated following Snedecor and Cochran (1967), to maintain a balanced design. A priori multiple comparisons were carried out as modified  $t$ -tests (Snedecor and Cochran 1967) for individually contrasting irradiation treatments with transport controls. Sample sizes for these tests ranged from 27 to 34. Transport and box controls were compared by paired  $t$ -tests (Snedecor and Cochran 1967). Sample sizes for these tests ranged from 10 to 15. All means are given with their standard errors.

## RESULTS

### HATCHING AND FLEDGING SUCCESS

The 35 clutches initially had an average of  $5.5 \pm 0.1$  eggs, giving rise to  $5.1 \pm 0.1$  hatchlings and  $3.7 \pm 0.3$  fledglings. This corresponds to an average breeding success of  $67.3 \pm 5.2\%$ , which is comparable to, and in many cases higher than, that of relatively undisturbed colonies (Low 1933, Kuerzi 1941, Chapman 1955, Rustad 1972).

Hatching success was similar for all the radiation treatments and the two control groups (Table 1). Two eggs disappeared from separate nests shortly after irradiation. They were likely damaged and then removed by one of the adults. A third egg was cracked by us during handling. Although 95.2% of the eggs placed into the incubator hatched, individual treatments had up to two eggs that did not hatch (Table 1). Of the nine eggs that did not hatch, four were infertile and five contained dead embryos, two of which had everted yolk sacs. This was likely caused by the artificial incubation (Kuehler Toone 1983). None of these observations appear to be related to radiation exposure.

Fledging success was similar for all the groups (Table 2). Individual groups lost up to six

TABLE 3. Mean observed growth statistics ( $\bar{x} \pm SE$ ) for nestlings from acutely irradiated eggs and unirradiated transport controls.

| Statistic <sup>a</sup>                | Control         | 0.4 Gy       | 0.8 Gy       | 1.6 Gy          | 3.2 Gy          |
|---------------------------------------|-----------------|--------------|--------------|-----------------|-----------------|
| Hatching body mass (g)                | 1.37 ± 0.02     | 1.37 ± 0.03  | 1.36 ± 0.02  | 1.37 ± 0.02     | 1.39 ± 0.02     |
| Body-mass asymptote (g)               | 22.91 ± 0.24*** | 22.28 ± 0.31 | 22.44 ± 0.41 | 21.65 ± 0.34*** | 20.10 ± 0.32*** |
| Fledging body mass (g)                | 19.97 ± 0.24*** | 19.69 ± 0.37 | 19.54 ± 0.29 | 19.44 ± 0.24    | 17.49 ± 0.36*** |
| Recession body-mass loss (g)          | 2.98 ± 0.25     | 2.75 ± 0.19  | 2.90 ± 0.32  | 2.56 ± 0.15     | 2.45 ± 0.28*    |
| Emergence primary-feather length (mm) | 0.66 ± 0.05     | 0.70 ± 0.06  | 0.78 ± 0.10  | 0.72 ± 0.06     | 0.71 ± 0.05     |
| Fledging primary-feather length (mm)  | 60.06 ± 0.85*** | 60.67 ± 0.56 | 59.80 ± 0.53 | 60.57 ± 0.78    | 57.10 ± 0.93*** |
| Fledging foot length (mm)             | 25.29 ± 0.17    | 25.22 ± 0.15 | 25.36 ± 0.13 | 25.19 ± 0.14    | 24.93 ± 0.20*   |
| Incubation time (d)                   | 16.19 ± 0.24*** | 16.16 ± 0.20 | 16.03 ± 0.20 | 16.11 ± 0.22    | 16.59 ± 0.19**  |
| Nesting time (d)                      | 20.31 ± 0.21    | 20.43 ± 0.16 | 20.42 ± 0.17 | 20.32 ± 0.22    | 20.10 ± 0.25    |
| Time to body-mass asymptote (d)       | 14.55 ± 0.28    | 14.50 ± 0.35 | 14.31 ± 0.30 | 14.71 ± 0.30    | 15.30 ± 0.34*   |
| Recession time (d)                    | 5.60 ± 0.32*    | 5.89 ± 0.36  | 5.68 ± 0.30  | 5.49 ± 0.28     | 4.72 ± 0.36*    |
| Time to primary-feather emergence (d) | 7.07 ± 0.14*    | 7.11 ± 0.10  | 7.27 ± 0.12  | 7.21 ± 0.14     | 7.50 ± 0.14***  |

<sup>a</sup> Probability levels associated with control values are for analysis of variance based on all the treatments, and those associated with irradiation treatments are for a priori multiple comparisons of each treatment vs. control. Means are based on 27 to 34 observations.

\*  $P < 0.05$ , \*\*  $P < 0.01$ , \*\*\*  $P < 0.005$ .

young, mainly to kestrels, which took relatively large nestlings by inserting a leg through next-box holes (see Zach and Mayoh 1984). A few small young that must have died in the nests were likely removed by one of the parents. In total, 23 young were lost from 16 nests, with up to 6 per group (Table 2). Mortality of nestlings unrelated to predation could have been radiation-induced, but was more likely due to exposure and starvation during several periods of cold, wet and windy weather. Under such conditions Tree Swallow nestlings can suffer very high mortality (Austin and Low 1932, Chapman 1955, Rustad 1972, Zach and Mayoh 1982b). Neither predation losses nor nest deaths appear to be related to radiation exposure (Table 2).

#### OBSERVED GROWTH STATISTICS

Many observed growth statistics differed statistically among the five treatments (Table 3). In all cases, nestlings had a similar hatching body mass, but subsequent growth was significantly depressed in the 1.6-Gy and 3.2-Gy young. The lower recession body-mass loss of the 3.2-Gy nestlings likely reflects their reduced body-mass asymptote, or the shortened recession time. The 3.2-Gy nestlings had significantly shorter feet and primary feathers at fledging. Radiation exposure also affected the timing of development. Hatching in the 3.2-Gy nestlings was significantly delayed, but the nestling time remained unaffected. However, the 3.2-Gy nestlings reached the body-mass asymptote significantly later and had a corresponding reduction in the recession time. They also had a significant delay in primary-feather emergence.

The results clearly show that exposure of eggs to doses of 1.6 and 3.2 Gy depressed nestling growth and delayed development. Apparently, doses up to 0.8 Gy had no effect on growth.

#### GROWTH-MODEL PARAMETERS

The percentages of variation explained by the Richards model for individual treatments ranged from  $99.5 \pm 0.0$  to  $99.7 \pm 0.0$  for body mass, from  $99.6 \pm 0.0$  to  $99.7 \pm 0.0$  for primary-feather length, and from  $99.1 \pm 0.1$  to  $99.4 \pm 0.1$  for foot length. These mean values are based on the variation in the observed data (Zach et al. 1984) and they indicate excellent fits. High explained percentages of variation are also indicative of randomly distributed residuals with homogeneous variances and, therefore, of unbiased fits (Zach et al. 1984). The transport controls grew most smoothly, having the highest mean explained percentages of variation in all cases.

The fitted growth-model parameters for body mass indicated significant growth depression in the 1.6-Gy and 3.2-Gy nestlings (Table 4), confirming the results from the observed growth statistics (Table 3). The predicted growth curves for the five treatments have unique shapes (Fig. 1), as suggested by the significantly different shape-parameter values (Table 4). Contrary to expectations from the observed growth statistics, none of the growth-model parameters for primary-feather length indicated significant radiation-induced growth depression. However, the predicted foot-length asymptote of the 3.2-Gy nestlings was significantly reduced, as expected.

The results show that exposure of eggs to doses of 1.6 and 3.2 Gy depressed nestling growth, particularly in body mass. Apparently, radiation had no consistent effects on the shape of the growth curves, even for body mass (Table 4).

#### TRANSPORT AND BOX CONTROLS

Transport and box-control nestlings grew similarly, although there were some significant differences in observed growth statistics and fitted model-parameter values (Table 5). Most important, transport controls had a significantly lower hatching body mass than box controls. Since the probability of finding hatchlings in a given time interval was similar for both control types, this difference is likely due to parental feeding of box controls immediately following hatching. Alternatively, transport controls may have become dehydrated following the significantly longer incubation time (Table 5). The transport and box controls also had significantly different predicted growth curves for primary-feather and foot lengths.

The results show that our experimental procedures had significant effects on hatching body mass and incubation time, independent of radiation exposure. These effects may have subtly affected subsequent growth.

## DISCUSSION

### BASIC RADIOBIOLOGICAL PRINCIPLES

Gamma radiation consists of energetic electromagnetic waves with short wave lengths and high frequencies. Low-level gamma radiation generated by cosmic rays, and from the decay of primordial and man-made radioisotopes, is ubiquitous in the environment (Upton 1982).

Gamma radiation is very penetrating. In biological material, it can bring about changes in the energy states of atoms and molecules and thereby cause chemical, somatic, and genetic changes that may interfere with normal functions (Whicker and Schultz 1982). The effects of gamma and x-, or Roentgen, rays are

TABLE 4. Mean parameter values ( $\bar{x} \pm \text{SE}$ ) from the Richards growth model fitted to nestlings from acutely irradiated eggs and unirradiated transport controls.

| Parameter                               | Dose (Gy)           |                  |                  |                   |                     |
|---|---------------------|------------------|------------------|-------------------|---------------------|
|   | Control             | 0.4 Gy           | 0.8 Gy           | 1.6 Gy            | 3.2 Gy              |
| Body-mass asymptote (g)                 | 24.42 $\pm$ 0.42*** | 23.52 $\pm$ 0.44 | 23.49 $\pm$ 0.55 | 23.39 $\pm$ 0.36* | 21.08 $\pm$ 0.40*** |
| Growth-rate constant (d <sup>-1</sup> ) | 0.44 $\pm$ 0.03**   | 0.47 $\pm$ 0.03  | 0.51 $\pm$ 0.04  | 0.38 $\pm$ 0.02   | 0.46 $\pm$ 0.03     |
| Shape parameter                         | 0.83 $\pm$ 0.12***  | 0.93 $\pm$ 0.14  | 1.13 $\pm$ 0.16* | 0.55 $\pm$ 0.09   | 1.06 $\pm$ 0.14     |
| Primary-feather length asymptote (mm)   | 67.09 $\pm$ 0.84    | 66.63 $\pm$ 0.79 | 65.80 $\pm$ 0.82 | 67.04 $\pm$ 1.14  | 65.22 $\pm$ 0.98    |
| Growth-rate constant (d <sup>-1</sup> ) | 0.30 $\pm$ 0.01     | 0.30 $\pm$ 0.01  | 0.31 $\pm$ 0.01  | 0.31 $\pm$ 0.01   | 0.30 $\pm$ 0.01     |
| Shape parameter                         | 0.25 $\pm$ 0.02     | 0.28 $\pm$ 0.03  | 0.26 $\pm$ 0.03  | 0.28 $\pm$ 0.04   | 0.25 $\pm$ 0.03     |
| Foot-length asymptote (mm)              | 26.04 $\pm$ 0.28    | 25.61 $\pm$ 0.21 | 25.90 $\pm$ 0.36 | 25.55 $\pm$ 0.28  | 25.27 $\pm$ 0.31*   |
| Growth-rate constant (d <sup>-1</sup> ) | 0.86 $\pm$ 0.10     | 0.93 $\pm$ 0.12  | 0.94 $\pm$ 0.12  | 0.94 $\pm$ 0.11   | 1.02 $\pm$ 0.17     |
| Shape parameter                         | 4.70 $\pm$ 0.62     | 5.04 $\pm$ 0.76  | 5.25 $\pm$ 0.83  | 5.14 $\pm$ 0.72   | 6.38 $\pm$ 1.36     |

\* Probability levels associated with control values are for analysis of variance based on all the treatments, and those associated with irradiation treatments are for a priori multiple comparisons of each treatment vs. control. Means are based on 27 to 29 observations.

\*\*  $P < 0.05$ , \*\*\*  $P < 0.001$ , \*\*\*\*  $P < 0.0005$ .

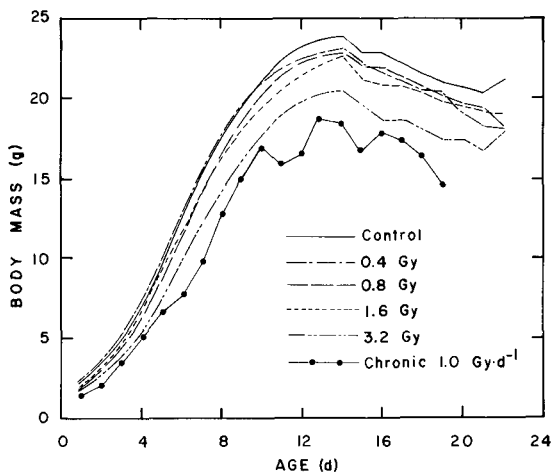


FIGURE 1. Body-mass growth curves for nestlings from eggs irradiated to 0.4, 0.8, 1.6 and 3.2 Gy, and from unirradiated transport controls. Up to day 14, the curves are those predicted by the Richards model. During mass recession beyond day 13, and for the entire curve of chronically irradiated nestlings, daily means are plotted. The parameter values for the curves are given in Table 4.

similar (Loken et al. 1960, Odum 1971). Among other factors, the amount of biological damage is a function of the total dose and the dose rate. All other things being equal, damage is correlated positively with total dose and negatively with dose rate (Stearner 1951, Stearner and Christian 1951). Thus, damage is reduced when a given total dose is spread over time. This is because, at low dose rates, biological repair mechanisms can partially or fully compensate for radiation-induced damage (Bedford 1982). In general, radiation effects are most pronounced between  $0.1 \text{ Gy} \cdot \text{h}^{-1}$  and  $60 \text{ Gy} \cdot \text{h}^{-1}$  (Hall 1972). We used an acute dose rate of  $216.0 \text{ Gy} \cdot \text{h}^{-1}$ , leaving total dose as the only important variable. Our radiation treatments ranging up to 3.2 Gy are substantial, approaching the 50% lethal dose ( $\text{LD}_{50}$ ) for mammals (Sparrow et al. 1967, Odum 1971).

#### MORTALITY

Our results clearly show that acute doses up to 3.2 Gy to partially incubated Tree Swallow eggs did not reduce hatching and fledging success (Tables 1 and 2). Further, radiation exposure did not increase vulnerability to kestrel predation (Table 2). These results confirm our earlier findings with acutely irradiated nestlings, that Tree Swallows (Zach and Mayoh 1984) and House Wrens (Zach and Mayoh 1986) are relatively insensitive to radiation exposure, as judged by mortality up to fledging.

Few comparative data for wild birds are available. Norris (1958) irradiated a few Eastern Bluebird (*Sialia sialis*) eggs, but sample sizes were too small to make statistically valid conclusions. Similarly, Wetherbee (1966) ir-

radiated eggs of several passerine species, but the hatching success under artificial incubation was abnormally low for treatments and controls alike.

Sensitivity to radiation exposure is closely correlated with cell differentiation and proliferation (Odum 1971, Whicker and Schultz 1982). Thus, radiosensitivity decreases from embryo to nestling to adult (but see Willard 1963). Adult passerines have  $\text{LD}_{50}$  values of about 8.0 to 10.0 Gy (Garg et al. 1964, Sturges 1968), which would constitute tremendously high doses in an ecological setting.

In the chick (*Gallus domesticus*) embryo, radiosensitivity, as measured by the  $\text{LD}_{50}$ , decreases from about 20.0 Gy for fresh eggs to 7.0 Gy on incubation day 8 and then gradually increases to 8.0 Gy towards hatching (Karnofsky et al. 1950, Geoff 1959, Muller and Moreng 1966, Wendt 1981). This suggests that radiation exposure on incubation days 7 to 8 in our study coincided with a relatively sensitive period. Changes in the radiosensitivity of the chick embryo are closely correlated with the formation of various organs and organ systems (Essenberg and Zikmund 1938, Geoff 1959, see also Hamilton 1952). However, very low radiation doses, up to about 0.1 Gy, may not be damaging in a conventional sense. Low doses may enhance embryonic development and hatchability (Essenberg 1935, Bless and Romanoff 1943, Kuzin et al. 1975). Our data for the 0.4-Gy treatment do not suggest any such enhancement (Tables 1 and 2).

Although there was no radiation-induced mortality in our study up to fledging, it is possible that such deaths occurred later (Prosser 1947). In irradiated chick embryos, acute deaths within about a day of exposure are mainly due to vascular injuries. Delayed mortality can be due to a variety of causes, including hemorrhage, general edema, necrosis, and abnormalities (Karnofsky et al. 1950, Geoff 1959, Moreng and Hollister 1963, Stearner and Christian 1969), none of which were observed in our fledglings. In theory, delayed mortality can be investigated via the return of banded nestlings during subsequent breeding seasons. Unfortunately, in our studies returns have been very low (see Zach and Mayoh 1984). In spite of a thorough search in 1985, we failed to locate any of the birds banded as nestlings in 1984, irrespective of treatment. Studies of adults, who have a strong tendency to return rather than disperse, may be more promising (Sheppard 1977, De Steven 1980).

#### GROWTH

Our results clearly show that acute doses of 1.6 Gy or more to partially incubated Tree Swal-

TABLE 5. Selected mean observed growth statistics and parameter values ( $\bar{x} \pm SE$ ) from the Richards growth model fitted to unirradiated transport and box controls.

| Statistic/parameter*                    | Transport control  | Box control      |
|---|--------------------|------------------|
| Hatching body mass (g)                  | 1.38 $\pm$ 0.03*** | 1.61 $\pm$ 0.05  |
| Incubation time (d)                     | 16.21 $\pm$ 0.21** | 15.64 $\pm$ 0.20 |
| Primary feather length                  |                    |                  |
| Growth-rate constant (d <sup>-1</sup> ) | 0.30 $\pm$ 0.02    | 0.29 $\pm$ 0.01  |
| Shape parameter                         | 0.29 $\pm$ 0.03*   | 0.21 $\pm$ 0.02  |
| Foot length                             |                    |                  |
| Growth-rate constant (d <sup>-1</sup> ) | 0.63 $\pm$ 0.10*   | 1.11 $\pm$ 0.14  |
| Shape parameter                         | 3.12 $\pm$ 0.70*   | 6.23 $\pm$ 0.96  |

\* Probability levels are for paired *t*-tests comparing the two types of controls. Means are based on 9 to 14 observations.

\*\*  $P < 0.05$ , \*\*\*  $P < 0.01$ , \*\*\*\*  $P < 0.005$ .

low eggs depresses subsequent growth in body mass and primary-feather and foot lengths (Tables 3 and 4). It also prolonged incubation time, time to primary-feather emergence, and time to body-mass asymptote. However, as indicated by the shape parameter of the Richards model, it did not affect basic growth patterns in a consistent way (Table 4). These results are in general agreement with those from our study with irradiated Tree Swallow nestlings (Zach and Mayoh 1984). Although direct comparisons are difficult to make, growth in the 1.6-Gy and 3.2-Gy treatments is comparable to that of nestlings irradiated with 2.7 and 4.5 Gy (Zach and Mayoh 1984). This suggests that 7 to 8 day old embryos are more radiosensitive than freshly hatched nestlings.

The prolonged incubation period induced by radiation exposure did not affect hatching body mass (Table 3). In radiation treatments and transport controls alike, hatching body mass was correlated positively with egg mass, with coefficients (*r*) ranging from 0.86 to 0.91 ( $P < 0.001$ ). However, in no case were asymptotic or fledging body masses significantly correlated with egg or hatching body masses. Apparently, radiation exposure did not affect these relationships.

We are unaware of any comparable growth data from incubated embryos of wild passerines. However, growth depression and increased incubation time have been noted in irradiated chick embryos (Essenberg 1935, Bless and Romanoff 1943, Muller and Moreng 1966, Tyler et al. 1967). We did not investigate the reasons for depressed growth and delayed development of Tree Swallow embryos and nestlings. These could include circulatory disturbances, renal failure, hepatic lesions, epithelial changes in the digestive system, and damage to hematopoietic tissues (Prosser 1947, Jacquez and Karnofsky 1950, Quastler 1956, Stearner and Christian 1972).

Besides slight stunting, which was not obvious to the casual observer, radiation expo-

sure had no other visible effects. Radiation-induced gross abnormalities are relatively uncommon in birds. Sandvik (1958) recovered 12 abnormal chick embryos from 1,300 eggs, induced by doses ranging up to 37.0 Gy. Moreng and Hollister (1963) irradiated 2,169 chicken eggs with up to 11.0 Gy and observed 9.2% abnormal embryos, mostly at the highest doses.

Results from chick embryos suggest that radiation-induced stunting is likely permanent (Muller and Moreng 1966, Tyler et al. 1967). Further, exposure to excessive radiation during embryonic development may lead to loss of, or reduced, fertility, particularly in females (Essenberg and Zikmund 1938; Muller and Moreng 1963, 1966; Hughes 1964; Mraz and Woody 1973).

Our results clearly show that fledging and hatching success and the occurrence of gross abnormalities are poorer indicators of radiation stress in birds than are growth data. Surprisingly, observed growth statistics (Table 3) appear to be more sensitive indicators than the fitted growth parameters from the Richards model (Table 4), in spite of an excellent fit. This also occurred in our previous irradiation studies using the logistic, Gompertz, and von Bertalanffy (Zach and Mayoh 1984), and the Richards model (Zach and Mayoh 1986).

#### TRANSPORT AND BOX CONTROLS

Besides radiation exposure, our experiment involved other potential stress factors that may have affected development and growth. Thus, the differences between the transport and box controls (Table 5) are not entirely unexpected.

Contrary to Mayoh and Zach (1985), laboratory hatching procedures in the present study prolonged incubation time and depressed hatching body mass, as indicated by the differences between the transport and box controls (Table 5). Artificial incubation can sometimes increase incubation time (Kuehler Toone 1983). We suspect that the transport controls

lost more body mass than expected from our previous study because we checked less frequently for hatchlings in the incubator due to the much heavier work load. Preliminary results with a few hatchlings showed that this did not cause serious dehydration. This suggests that the box controls gained body mass due to feeding immediately following hatching, whereas the transport controls did not. Clearly, experimental stress factors other than radiation exposure affected hatching and subsequent growth, as indicated by the fitted parameters from the Richards growth model. Unfortunately, little is known about the interaction of various stress factors, and one can only guess how stress from artificial hatching procedures interacted with radiation effects.

Our results demonstrate that multiple controls are essential for meaningful interpretation of complex field experiments. It may also be argued that such experiments belong in the domain of the laboratory. However, we strongly feel that potential man-made environmental stresses must be studied in an ecological setting to assess their full impact.

#### CHRONIC IRRADIATION

In an ecological setting, chronic low-level radiation exposure may be more relevant than the acute high levels used in our study. Unfortunately, chronic field studies are very difficult to conduct because of their need for large irradiators (Turner 1975, Whicker and Schultz 1982). An alternative might be the use of injected or ingested radionuclides (Warren and Dixon 1949). In essence, many studies involving radioactive tracers in animals could be interpreted as low-level chronic exposure studies.

From one of our field irradiators (Zach and Mayoh 1982a, Guthrie and Dugle 1983), we have collected data over several years on four Tree Swallow nests exposed to doses of about  $1.0 \text{ Gy} \cdot \text{d}^{-1}$ , or totals of about 16.0 and 20.0 Gy for the incubation and nestling periods, respectively. Of the 24 eggs laid, only 13 hatched, which gave rise to 11 fledglings. The hatching success of  $56.3 \pm 14.7\%$  was unusually low (Table 1), whereas the fledging success of  $88.8 \pm 6.6\%$  appears to have been unaffected by radiation exposure (Table 2). However, growth depression under chronic exposure to a dose of  $1.0 \text{ Gy} \cdot \text{d}^{-1}$  was far more severe than for our 3.2-Gy treatment (Fig. 1). Results for House Wrens were similar (Zach and Mayoh 1986). These data show that nestling growth is the most sensitive indicator of radiation stress, followed by hatching and finally fledging success.

#### ENVIRONMENTAL PROTECTION

In radiation protection of the environment, it has been assumed that man is the most sensitive link and that stringent protection of man will also suffice for other organisms and the environment at large (Loutit 1956, Taylor 1971, NAS 1972, ICRP 1977, Whicker and Schultz 1982). Considering the history of some chemical pollutants and birds (Hickey and Anderson 1968, Fleming et al. 1983, Peakall and Bart 1983), this broad generalization should not go unchallenged (Odum 1971).

Thus far, we have used external acute gamma-radiation doses of up to 6.0 Gy with bird embryos or nestlings without inducing any mortality. Since the  $LD_{50}$  for adult man is about 5.0 Gy (Rees 1967), our results suggest that radiation protection for man, who is relatively long-lived, is more than adequate for wild birds such as Tree Swallows and House Wrens. There is no need for separate limits (Whicker and Schultz 1982).

However, more field studies are needed to determine the effects of stress factors brought about by man's activities. Traditionally, such studies have documented existing problems and recommended remedial actions. This is often ineffective. Future studies should keep pace with new technological developments and should anticipate potential environmental problems, to allow effective input on limits and safety standards, and even on the direction of man's future activities.

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