REP 1993 - 024

Arch. Environ. Contam. Toxicol. 25, 192–203 (1993)

ARCHIVES OF
Environmental
Contamination
and Toxicology
© 1993 Springer-Verlag New York Inc.

Effects of DDE and Food Stress on Reproduction and Body Condition of Ringed Turtle Doves

James O. Keith and Christine A. Mitchell[1]

Denver Wildlife Research Center, U.S. Department of Agriculture, P.O. Box 25266, Denver, Colorado 80225-0266, USA

Abstract. Six trials with ringed turtle doves (*Streptopelia risoria*) explored the combined effects of food restrictions and DDE [1,1,-dichloro-2,2- bis(*p*-chlorophenyl) ethylene] on reproductive performance and body condition. In each trial, eight groups of eight breeding pairs were either exposed (four groups) or not exposed (four groups) to DDE and held on either 100, 90, 80, or 70% of normal food intake. Three performance trials and three condition trials were conducted. In each case, the three trials differed only in the time food was restricted—either 2 weeks before pairing, at pairing, or at egg laying. Performance trials assessed reproductive performance and were continued for about 42 days, the normal period required to fledge young. Condition trials were each terminated at the time most pairs failed in the corresponding performance trial. Pairs were then sacrificed to assess their body condition. In performance trials, treatments severely affected breeding success. Overall, in the three trials, productivity in clean birds was reduced 50, 85, and 100%, respectively, at food intakes of 90, 80, and 70% of normal. Effects were greater on DDE birds; productivity was lowered 23, 87, 98, and 100% at 100, 90, 80, and 70% food intake, respectively. The timing of food restriction was as important as its intensity. A 10% reduction in food before pairing had a greater effect on overall performance than a 30% reduction at egg laying. DDE effects were greatest in birds subjected to food restrictions before egg laying. Treatments affected females more than males. In performance trials, productivity was reduced by nonbreeding and by increased death of embryos and young due to inadequate brooding and care. In condition trials, body condition was not greatly affected by treatments. Losses in body weight and in fat and protein reserves were not as closely related to breeding performance as were reduced size of gonads and crop glands. Treatments apparently restricted breeding success by limiting the levels of hormones necessary to develop and maintain active gonads, adequate courtship and brooding behavior, and functional crop glands. Food is constantly a limiting factor for wildlife. Further reductions in food supplies caused by human activities along with chemical contaminants in the environment can be expected to adversely influence reproductive success and pose serious restrictions on avian populations.

Numerous studies over the last several decades have shown that insecticides can adversely affect avian reproduction (see reviews by Brown 1978, Peakall 1985, Smith 1987, Peterle 1991). DDE, the most abundant metabolite of DDT in the environment, reduced eggshell thickness and decreased reproductive success in avian predators (Hickey and Anderson 1968, Peakall 1970). Species such as the peregrine falcon (*Falco peregrinus*), brown pelican (*Pelecanus occidentalis*), bald eagle (*Haliaeetus leucocephalus*), and osprey (*Pandion haliaetus*) became endangered due to DDE effects on their populations.

Long-term studies of brown pelicans in the Gulf of California, Mexico, by the authors, as well as K. A. King and D. W. Anderson, identified reproductive problems under conditions of both DDE exposure and food stress. Pelican reproductive success varied annually. Productivity was good in some years, but in other years pelicans either failed to breed or after mating they deserted nests and abandoned eggs and young. DDE residues in adipose tissue of breeding pelicans ranged up to 2050 ppm. Feeding success was monitored, and nest desertion primarily occurred during periods of food scarcity. Results of pelican studies will be reported elsewhere; the research reported here was designed to experimentally simulate conditions to which pelicans were subjected; the objective was to test the null hypothesis that effects of food restrictions and DDE are not additive in contributing to reproductive debility when birds are concurrently challenged by both factors.

Ringed turtle doves were chosen, because their breeding biology is more similar to those of brown pelicans than any other experimental species. Pelicans and doves are monogamous, determinate layers, produce a small clutch, and have an extensive repertoire of reproductive behavior. Both sexes participate in incubation and brooding of young, which are altricial and require prolonged care. Breeding ringed turtle doves are tractable and not easily disturbed by human activity. The care, behavior, and reproductive biology of ringed turtle doves have been described (Miller and Miller 1958; Lehrman 1965; Lehrman and Wortis 1967). The use of prescribed maintenance

[1]Present address: U.S. Fish and Wildlife Service, La Crosse, WI 54602.

Table 1. Description of the six experimental trials

Timing of food restrictions	Performance trials		Condition trials	
	Trial no.	Duration[a]	Trial no.	Duration[a]
Two weeks before pairing	1	10 weeks	4	8 days
At pairing	2	10 weeks	5	14 days
At egg laying	3	8 weeks	6	30 days

[a] Period between pairing and termination of trial. In Trials 1 and 4, food was restricted a total of 12 weeks and 22 days, respectively

techniques ensured consistently good performance and productivity against which to test the effects of food restrictions and exposure to DDE.

Methods

Experimental Design

Two sets of trials were conducted—three performance trials and three condition trials. In performance trials, doves were paired and their reproductive progress was evaluated until control birds had fledged their young. In condition trials, birds were sacrificed at the time doves showed reproductive problems in the performance trials; features of body condition were then measured.

Brown pelicans were influenced more during reproduction by DDE residues accumulated in their bodies than by DDE in the food they ate while reproducing (Keith 1978). To simulate this condition, doves assigned to DDE treatments were fed DDE contaminated diets prior to experiments to establish body residues of DDE. All doves were fed uncontaminated food during the reproductive trials. Wild birds can experience food shortages at any time before or during the breeding season. The timing of such stress can contribute to the failure of some adults to breed, to the desertion of eggs and nestling after nests are established, and to starvation of older young before fledging. To simulate such conditions, three types of trials were conducted that differed only in the time at which food was restricted. These three types of trials were conducted in both performance trials (1, 2, and 3) and condition trials (4, 5, and 6). In Trials 1 and 4, food restrictions began 2 weeks before doves were paired for reproduction. Those trials tested the effects of food restrictions on birds that had not initiated breeding. Food was restricted at the time doves were paired for reproduction in Trials 2 and 5 to look at effects during courtship and egg laying. Finally, in Trials 3 and 6, food for each pair was restricted on the day after they laid their first egg. Those trials tested treatment effects on birds during incubation and rearing of young. In all trials, food restrictions were continued until the trials were terminated. The timing of food restriction and duration of each trial are given in Table 1.

Wild birds can be subjected to different intensities of food shortages. To span the range of likely food restrictions, groups of doves were maintained on 70, 80, 90, and 100% of normal food consumption. These levels of food restriction were imposed in each of the six trials. Normal consumption was the weight of food eaten by the 100% group, fed *ad libitum*.

Each trial was an eight-celled experiment. In addition to the four levels of food availability (70, 80, 90, and 100% of normal), two DDE conditions were established in doves—none (0), also referred to as clean, and DDE (X). Treatment groups were designated by their DDE exposure and their level of food availability (e.g., X-100 and 0-90). In all trials, eight pairs of doves were subjected to each of the eight treatments, except Trial 4. Because none of the clean or DDE pairs at the 70 or 80% level of food availability made an attempt to reproduce in Trial 1, the 70% treatment was omitted in the corresponding condition trial (Trial 4).

Treatment of Doves

For each trial, adult doves (128) that had previously produced young were visually isolated from each other for 6 weeks by keeping males (64) and females (64) in separate rooms. Protocols and maintenance procedures followed those of Lehrman and Wortis (1967). During the first 3 weeks of isolation, half of the males (32) and females (32) were fed pelleted food containing 100 ppm (dry weight) DDE to establish residue burdens in their bodies. Based on food consumption while on DDE diets, both males and females ingested between 20 and 30 mg of DDE. During the last 3 weeks of isolation and for the remainder of each trial, all birds were fed clean food. In Trials 1 and 4, food was restricted 2 weeks before pairing of birds for reproduction; those treatments were imposed during the fifth and sixth weeks of isolation. In other trials, all birds were fed *ad libitum* during isolation, and food restrictions were imposed either at pairing (Trials 2 and 5) or at egg laying (Trials 3 and 6). Food restrictions and pairing of birds for trials were assigned randomly. Pairs were randomly placed in one of 72 cubicles (80 × 40 × 30 cm with wire fronts) in six batteries. Water, food (clean, pelleted pigeon chow), grit, nest bowls, and nest material (pine needles) were provided and a daily photoperiod (10 D : 14 L) was maintained. During trials, food consumption was measured daily for pairs fed *ad libitum* (0-100 and X-100). Each week, average consumption was determined for those pairs and, if necessary, adjustments made in amounts being fed to birds on food restrictions. After food restrictions were imposed, food for birds on reduced intake was weighed out and fed each morning. As young grew after hatching, food consumption of control pairs slowly increased until it almost doubled. Amounts fed to pairs on restricted diets were increased proportionately.

Nesting Data

After doves were paired, nesting progress was recorded daily. Nest construction, which took place over several days, was scored on a scale of 0, 1, 3, or 5, indicating increasing quantities of nest material in nest bowls. The number of eggs and young in nests was recorded each day. Eggs found out of nests were removed and examined to determine the day of embryo death. Young found out of nests were not replaced. Dead young were removed from nests and cubicles, and day of death was recorded.

A performance index was calculated for each pair in each trial to depict the degree of effort they gave to reproduction. This index was the sum of the daily numbers of viable eggs or young that were present in the nest of a pair during the first 42 days after pairing in performance trials or until the trial was terminated in condition trials. The 42-day period provided enough time for doves to complete their normal reproductive cycles. Eggs usually were laid within 7 days after pairing, incubation required 14 days, and young fledged at 21 days of age. Performance indices allowed use of a two-way analysis of variance to test the interactions between food restrictions and DDE on nesting data. Interaction effects cannot be determined in nonparametric analyses, which would be required for data on numbers of eggs laid and hatched, and numbers of young fledged.

Behavioral Data

Courtship behavior and nesting behavior were observed and recorded each weekday morning during performance trials until all young were fledged, and during condition trials, until the trials were terminated.

Observers scanned each battery of 12 cubicles for 30 min while sitting about 4 m in front of the battery. Behavior of doves, by sex, was tallied or timed. Males were marked for identification with red dye on their shoulders. A behavior score was determined for every bird and every pair each day on the basis of recorded observations. Scores for each type of display increased with the number of bouts exhibited or the length of time the activity was continued. Scores for all displays were summed to obtain a total or daily score. The purpose of scoring was to derive a quantitative assessment of each pair's progress in the breeding cycle; for emphasis, behavior scores were cumulated over time as pairs progressed from courtship to incubation and to care of young (see Keith 1978).

Condition Data

Body weights of adults were obtained during isolation and each trial. When condition trials ended, birds were weighed, killed, plucked, and reweighed. The left testis of males and the ovary and oviduct of females were excised and weighed. A sample of abdominal mesenteric fat was taken from all birds in Trial 4 and from clean birds in Trial 5. The abdominal fat pad, as well as the left breast muscles, was excised from the DDE birds in Trial 5 and from all birds in Trial 6. Adipose samples, fat pads, and breast muscles were weighed. In Trial 6, crops were removed from all birds and weighed. Crops, breast muscles, gonads, and oviducts were ground with carcass remainders for residue analyses.

Residue Analyses

Adipose samples and 20 g aliquots of ground carcasses were analyzed for DDE residues and lipid content by Raltech Scientific Services Inc, Madison, WI. Tissues were mixed with sodium sulfate, air dried, desiccated overnight, extracted in Soxhlet thimbles with 50:50 ethyl ether petroleum ether for 8 h, and concentrated. Aliquots for DDE determination were eluted with 1:20 ethyl ether in petroleum ether on a Florisil® column, concentrated, and redissolved in petroleum ether. Aliquots were injected on a Hewlett Packard Model 5710A electron capture gas chromatograph with a glass column (4 mm × 3.66 m) packed with 3% OV-1 on 80/100 Supelcoport. Temperatures were: column 220° C, injector 250° C, and detector 300° C. In text and tables all DDE residues are expressed in parts per million, wet weight. Values for percent lipids are the percentage by weight that lipids constituted of a wet-weight sample of tissue or aliquot of the homogenate of the whole, plucked carcass.

Statistical Analyses

Most data obtained on individual birds and pairs were subjected to either a two- or three-way analysis of variance with replicates. Weight data were analyzed with a four-factor analysis of variance with repeated measures. Tukey's Q mean separation tests were used to determine differences between means with equal sample sizes (Steel and Torrie 1960). In the tables, letters in parentheses [(a), (ab), (b), (bc), etc.] are used to indicate significant differences among food treatments (100, 90, 80, and 70%) and food × DDE interactions (0-100, X-100, 0-90, X-90, 0-80, X-80, 0-70, and X-70). Means with different letters differed significantly from each other at the stated probabilities. Real differences between DDE treatments (0,X) and sex (♂, ♀) are reported, but needed no mean separation tests. In tables, results of mean separation tests are given for main effects (food, DDE) and their interaction (food × DDE) only when $P < 0.100$. If interactions were significant, main effects often are not discussed. The objective of this study was to examined the interaction of DDE and food restriction; the individual effects of DDE and food restriction were of interest, but of less priority. Interactions cannot be determined for proportional data (e.g., hatching and fledging success), and those data were not analyzed. However, such data contributed to performance indices, which were analyzed to determine treatment interactions.

Comparability of Performance and Condition Trials

One of the first assessments after finishing the condition trials was to determine how closely they replicated the performance trials. To relate reproductive performance in performance trials with body and reproductive condition in condition trials, it was essential to confirm that the two sets of trials had proceeded similarly and to see if the same reproductive effects were obtained by repeating the experiments since reproducibility is perhaps the most stringent test of validity in scientific experiments.

Results

Food Restricted before Pairing (Trials 1 and 4)

In Performance Trial 1, doves assigned to food restrictions had been on limited food intake for 2 weeks before they were paired. Upon pairing, birds on 100% food (0-100 and X-100) responded immediately with courtship displays and acquired higher scores ($P = 0.039$) than other groups for courtship behavior (Table 2). Of birds on food restriction, only four pairs in the 0-90 group and 1 pair in the 0-80 group showed a real behavioral response to pairing. All other birds on food restriction displayed infrequently, received low scores for the courtship period, and failed to lay eggs (Table 2). DDE alone (X-100 group) did not influence reproductive behavior. However, a 10% food reduction decreased the intensity of behavior in clean birds (0-90) and practically eliminated it in DDE birds (X-90). Greater food restrictions severely reduced behavior in pairs, regardless of DDE treatments.

Most pairs began some nest building during the first 10 days after pairing, but scores for the ultimate quality of nests showed that only pairs in the 0-100, X-100, and 0-90 groups constructed reasonable nests (3.0 or better). Only five of the 48 pairs subjected to food restriction laid eggs, and none of those were DDE pairs. Although all five pairs incubated successfully and hatched their eggs, only about half of their young fledged (Table 2). Apparently reduced food intake by adults had an effect shortly after they began feeding young. Five young died in nests, and only four young ultimately were fledged by pairs on food restriction.

The performance indices reflected overall performance of treatment groups. DDE birds performed more poorly than clean birds ($P = 0.002$). All DDE pairs on food restrictions failed to produce eggs and therefore had zero indices. The X-100 group had a lower average index than the 0-100 group ($P = 0.002$). Analyses also indicated that pairs on 100% food performed better than all groups on food restriction ($P < 0.001$). Trial 1 showed that food restriction before pairing had severe effects on productivity in clean birds and precluded reproduction in birds carrying DDE residues.

Condition Trial 4 was terminated 8 days after doves were paired. This was done because, in Performance Trial 1, doves in most treatment groups had ceased to exhibit normal behavior

Table 2. Reproductive performance of doves in Trial 1 (food restriction 2 weeks before pairing)

Food intake (%) and DDE	Courtship behavior scores[a]		Egg laying		Eggs hatched		Young fledged		Performance index[b]	
			No. pairs	No. eggs	No. eggs	%	No. young	%		
100									(a)	
None	22.1	1.2 (a)	8	16	13	81	13	100	56.0	4.4
DDE	19.6	1.3 (a)	8	15	13	87	11	85	39.8	8.1
90									(b)	
None	12.9	3.0 (b)	4	8	7	88	3	43	24.4	9.6
DDE	4.5	0.7 (c)	0	0	0	0	0	0	0.0	—
80									(b)	
None	4.8	1.9 (c)	1	2	2	100	1	50	6.8	6.8
DDE	3.6	1.2 (c)	0	0	0	0	0	0	0.0	—
70									(b)	
None	2.0	0.3 (c)	0	0	0	0	0	0	0.0	—
DDE	1.8	0.7 (c)	0	0	0	0	0	0	0.0	—

[a]Data are $\bar{x}$ and SE for eight pairs. $P = 0.039$ for food × DDE interaction
[b]Data are $\bar{x}$ and SE for eight pairs. $P < 0.001$ for food effects; $P = 0.002$ for DDE effects; there were no significant interactions

Table 3. Average measurements of gonads and oviducts for doves in Trial 4 (food restricted 2 weeks before pairing and trial terminated 8 days after pairing)[a]

Food intake (%) and DDE	Testis weight[b] (g)		Ovary weight[c] (g)		Oviduct weight[c] (g)	
100	(a)					
None	0.47	0.04	0.73	0.19 (a)	2.67	0.56 (a)
DDE	0.50	0.04	0.38	0.10 (b)	1.13	0.50 (b)
90	(b)					
None	0.30	0.04	0.16	0.02 (b)	0.13	0.01 (b)
DDE	0.26	0.07	0.20	0.06 (b)	0.27	0.15 (b)
80	(b)					
None	0.23	0.03	0.13	0.01 (b)	0.15	0.01 (b)
DDE	0.27	0.09	0.14	0.01 (b)	0.14	0.03 (b)

[a]Data are $\bar{x}$ and SE for eight pairs
[b]$P < 0.001$ for food effects; there were no significant DDE effects or interactions
[c]$P = 0.062$ (ovary weight) and $P = 0.019$ (oviduct weight) for food × DDE interaction

by the end of the first week after pairing. An analysis of variance of behavior scores during the first week after pairing in Trials 1 and 4 showed no significant differences ($P = 0.422$) between trials or the interaction of trials with other main factors. At termination of Trial 4, seven of the eight control females (0-100 group) had eggs or enlarged (> 5.0 mm) follicles, whereas only four of the 40 females on treatments had progressed into egg production. This performance was similar to that in Trial 1 and suggested that the two trials had progressed similarly during the first 8 days after pairing.

Food restrictions significantly reduced testicular development in males ($P < 0.001$), but DDE had no effects (Table 3). In females, the interaction of food and DDE treatments had significant effects on weights of ovaries and oviducts. Ovaries ($P = 0.062$) and oviducts ($P = 0.019$) in all groups on treatments weighed significantly less than those of the 0-100 controls. In general, the pattern of treatment effects on gonads and oviducts of pairs in Trial 4 was similar to that seen for performance and behavior of pairs in Trial 1. Low ovary and oviduct weights in X-100 females may have resulted from an effect of DDE in delaying ovulation. In Trial 1, all X-100 females laid eggs, but, on the average, they took about 5 days longer than the 0-100 females to do so.

Body weights were measured five times during Trial 4. An analysis of variance indicated significant differences ($P < 0.001$) over time due to DDE, to food intake, and to sex. However, at termination of the trial, there were no real differences in average weights of males (range 145–149 g) due to either DDE or food intake levels. In contrast to males, average weights of females on the three levels of food intake did differ at termination. Weights decreased as food restrictions increased (average body weights were 148, SE 2.6; 142, SE 3.1; and 136, SE 3.4 g; at 100, 90, and 80% food intake, respectively). Only X-80 females weighed less (2 g) at termination than when food restrictions were begun.

Although some differences in body weights were present at the end of Trial 4, no real differences in the lipid content of whole carcasses were found between sexes or treatment groups (range 7.3–10.4%). The lipid content of adipose tissue actually tended to increase with greater food restriction and the 80% groups (65.2%) had significantly higher levels ($P = 0.039$) than the 100% groups (56.6%). Body weights of females decreased with food restrictions, but lipid content of carcasses and adipose tissue did not. This suggested that weight loss might have been due to loss of muscle tissue. It was decided, therefore, to weigh breast muscles in future condition trials. DDE residues in carcasses were similar in all birds exposed to DDE regardless of the level of food restrictions to which they had been subjected (range 64, SE 7.1 to 88, SE 12.0 ppm). Adipose DDE residues were higher ($P = 0.077$) in the 100% group (690, SE 82.0 ppm) than in the 90% group (516, SE 81.5 ppm). The 80% group was intermediate (569, SE 58.7 ppm) and not different from the other two groups.

Severe reproductive impairment was produced by treatments in Trials 1 and 4. Behavior scores and performance seemed related to gonad size and perhaps female body weights, but not to lipid reserves and DDE residues, suggesting that reproductive performance was mediated more by gonad function and factors controlling gonad development than by energy reserves

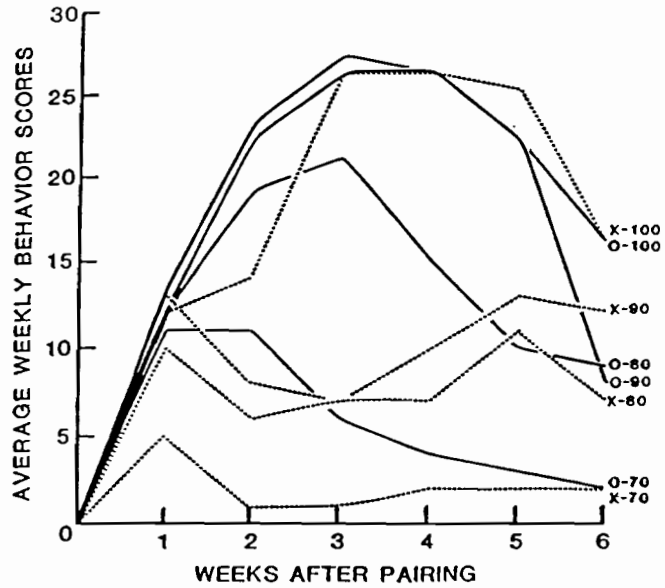

Fig. 1. Average weekly behavior scores for treatment groups in Trial 2 (food restriction at pairing)

and gross body condition. Although birds were on food restrictions for 22 days, most groups weighed as much or more at termination as when restrictions were begun. Body lipids were actually higher in groups on restricted diets than in controls. It seemed likely that treatments suppressed functions of the endocrine system related to gonad development and courtship behavior without diminishing energy reserves or compromising the body condition of doves.

Food Restricted at Pairing (Trials 2 and 5)

In Performance Trial 2, food restrictions were imposed the same day that birds were paired for reproduction. Upon pairing, most pairs immediately began courtship behavior. However, a lack of courtship the following day in six pairs in the X-70 group, and one pair in both the 0-70 and the X-80 group, indicated a quick and decisive reaction to treatments. Birds in those pairs did not respond to the presence of a mate. They seldom displayed and received low behavior scores from the beginning of the trial. After the first week the X-70, X-80, and X-90 groups ceased normal intensity of courtship behavior (Figure 1). Scores fell drastically after week 2 in the O-70 group and after week 3 in the O-80 group. The O-90, O-100, and X-100 groups performed better and had similar behavior scores.

Courtship behavior scores predicted the performance of experimental groups (Table 4). As behavior scores progressively decreased, pairs and groups ceased normal reproductive activities. In Trial 2, DDE birds took longer than clean birds to start their nests and lay eggs. The quality of nests was poorest in the O-70, X-70, and X-80 groups, and many of those pairs did not lay eggs. In Trial 2, food restriction had the greatest effects on DDE birds (Table 4); fewer DDE pairs laid eggs and their hatching success was poorer. A 10% food restriction at pairing did not affect the number of clean pairs (O-90) that laid, but the same food stress on DDE birds (X-90) reduced the number of laying pairs by one-half. Food restriction reduced egg hatchability in clean birds, and effects were more severe in birds with DDE residues.

Food limitations also lowered fledging success in clean birds compared to controls (0-100). Fledging rates were 22% lower in the O-90 group and 68% lower in the O-80 group. The 24 clean pairs on food restriction produced fewer young than the eight clean pairs on 100% food (12 vs 14). Again, as in Trial 1, no pairs subjected to the stresses of both DDE and food restriction produced young. Although DDE alone (X-100) lowered hatching success, it did not reduce fledging success. Overall performance, as indicated by performance indices, was increasingly reduced by each greater intensity of food restriction (Table 4). DDE pairs performed more poorly than clean pairs at all food levels ($P < 0.001$). Trial 2 illustrated the relative and combined effects on dove reproduction of DDE and food restrictions. Food restrictions imposed when birds were paired for reproduction seriously reduced productivity in clean birds and caused total failure in DDE birds.

Condition Trial 5, which likewise had food restrictions imposed at pairing, was terminated 2 weeks after pairing. Behavior score during those 14 days and scores attained by doves during the same period in Trial 2 were analyzed. None of the interactions between trials and other main factors (food and DDE) were significant, which implied that similar trends in behavior were established by food and DDE treatments in both trials. In the two trials, performance decreased with increasing food restrictions, and effects were most severe in DDE birds. In both trials, most pairs had built nests (54 of 64 in Trial 2 and 53 of 64 in Trial 5). This suggested a lack of impairment in males as they were primarily responsible for nest building. In contrast, few females in the X-90, X-80, O-70, and X-70 groups laid eggs (five of 32 in Trial 2 and seven of 32 in Trial 5), suggesting females were debilitated by those treatments.

In Trial 5, testis ($P = 0.006$), ovary ($P = 0.025$), and oviduct ($P = 0.024$) weights were two to three times heavier in the 100% group than in the 70% group. Weights in the 80 and 90% groups were intermediate and were not different from those in other groups. Analyses did not indicate effects due to DDE or to the interaction of food intake and DDE.

At termination of the trial, DDE birds had a lower average body weight (141, SE 1.5; $P < 0.001$) than clean birds (145, SE 1.3 g); body weights for the four food intake levels differed in both sexes at termination of the trial ($P = 0.010$). At 100 and 70% food intake, average weights were 155, SE 3.1 and 137, SE 2.4 g for males and 150, SE 2.8 and 132, SE 4.2 g for females, respectively. Males and females in the 80 and 90% intake groups had similar and intermediate weights.

Breast muscles were weighed from only DDE birds in Trial 5. Clean birds had been processed before the decision was made to assess treatment effects on breast muscle weights. Breast muscle weights did not differ between sexes but did decrease ($P < 0.001$) with increasing food restriction (14.8, SE 0.3; 13.6, SE 0.5; 13.6, SE 0.6; and 12.4, SE 0.4; respectively, at 100, 90, 80, and 70% food intake). The percentage of lipids in carcasses and in adipose tissue also decreased with increased food restriction ($P < 0.001$). Respective percentages in the 70% (7.1, SE 0.8 and 42.4, SE 4.8) and 80% (7.4, SE 0.6 and 42.0, SE 4.6) food groups were lower than those in the 100% group (9.9, SE 0.7 and 57.7, SE 3.6), and intermediate levels occurred in the 90% group (8.8, SE 1.1 and 50.6, SE 4.8). DDE birds had lower lipid levels than clean birds ($P < 0.001$),

Table 4. Reproductive performance of doves in Trial 2 (food restriction at pairing)

Food intake (%) and DDE	Courtship behavior scores[a]		Egg laying		Eggs hatched		Young fledged		Performance index[b]	
			No. pairs	No. eggs	No. eggs	%	No. young	%		
100	(a)									
None	16.5	1.7	8	16	15	94	14	93	66.5	1.9 (a)
DDE	15.2	0.8	8	15	9	69	9	100	45.0	8.0 (bc)
90	(a)									
None	16.2	1.3	8	16	14	88	10	71	54.8	6.5 (ab)
DDE	11.9	1.6	4	8	5	63	0	0	8.6	3.7 (d)
80	(a)									
None	14.7	2.1	7	14	8	57	2	25	32.5	7.1 (c)
DDE	8.2	2.0	1	2	0	0	0	0	0.8	0.8 (d)
70	(b)									
None	9.2	2.8	3	6	1	17	0	0	4.0	3.0 (d)
DDE	2.0	0.5	0	0	0	0	0	0	0.0	—

[a]Data are $\bar{x}$ and SE for eight pairs. $P < 0.001$ for food effects and for DDE effects; there were no significant interactions
[b]Data are $\bar{x}$ and SE for eight pairs. $P < 0.001$ for food × DDE interaction

but the interaction between DDE and food restriction was not significant. In Trial 5, DDE residues in carcasses and adipose tissue did not differ significantly between sexes or among food intake levels. As in Condition Trial 4, average residues varied considerably among all experimental groups (59, SE 7.5 to 88, SE 11.6 ppm in carcass and 435, SE 100 to 701, SE 151 ppm in adipose tissue).

In summary, treatment effects on behavior and performance were considerable in Trial 5 and were similar to those observed in Trial 2. Food restrictions caused a significant response in all attributes of condition that were measured, except for DDE residues. DDE treatment effects were most evident on behavior, performance, and weights of ovaries and oviducts in females.

Food Restricted at Egg Laying (Trials 3 and 6)

In Performance Trial 3, all treatment groups obtained similar behavior scores during the courtship period (Table 5). Food restrictions had not been imposed, and DDE treatments alone did not influence courtship behavior. After food restrictions were imposed at egg laying, pairs on 70% food intake accumulated lower scores ($P < 0.001$) during incubation than pairs on other food levels. Scores for 10 of 16 pairs on 70% food dropped nearly to zero during late incubation. DDE treatments did not affect behavior during incubation. In all groups on food restriction, behavior scores steadily decreased during care of young and were lower ($P < 0.001$) than those for pairs on 100% food intake. Similarly, groups on 70 and 80% food intake had lower scores than those on 90% food intake. DDE pairs tended to have lower scores than clean pairs, but those differences were not significant ($P = 0.132$).

As food restrictions were not imposed in Trial 3 until pairs had laid their first egg, the nest and egg data gathered were for 32 pairs of clean birds and 32 pairs of DDE birds. There were no differences between clean and DDE pairs in the time to first nest construction, the quality of the nest, or the number of pairs that laid eggs. A delay in laying (12.6 vs 10.2 days) and a slightly reduced clutch (1.9 vs 2.0 eggs) was evident in DDE birds (Table 6). These results generally are consistent with those in Trials 1 and 2 for groups that were not subjected to food restriction (0-100 and X-100 groups).

Table 5. Average behavior scores by periods and treatments for Trial 3 (food restriction at egg laying)[a]

Food intake (%) and DDE	Behavior scores by periods					
	Courtship		Incubation[b]		Care of Young[b]	
100			(a)		(a)	
None	20.9	1.4	27.3	0.4	22.7	1.2
DDE	22.1	0.9	27.1	0.2	17.9	2.8
90			(a)		(b)	
None	19.9	1.8	26.5	0.4	12.5	2.7
DDE	21.4	1.1	25.9	0.4	9.0	3.0
80			(a)		(c)	
None	19.8	1.8	22.2	2.6	3.8	1.5
DDE	17.9	1.4	25.4	0.5	4.9	2.3
70			(b)		(c)	
None	19.4	1.3	18.2	2.8	2.8	1.4
DDE	20.9	0.8	18.6	1.6	0.8	0.8

[a]Data are $\bar{x}$ and SE for eight pairs. Courtship extended between pairing and egg laying, incubation for the next 14 days, and care of young for 21 days after eggs hatched
[b]$P < 0.001$ for food effects; there were no significant DDE effects or interactions

When food restrictions were imposed as pairs laid their eggs, the resulting stresses depressed hatchability and survival of young (Table 6). The performance indices, which summarized those aspects of performance, showed the 100% group did better ($P < 0.001$) than those for the 70 and 80% groups. The effects of DDE were not as marked as in other trials. Hatchability appeared reduced by DDE in the 70 and 90% groups, as did fledgling in the 80% group, but analyses of performance indices indicated effects only from food restriction. Food restriction, even when delayed until egg laying, severely reduced nesting success. The 48 pairs on restricted food fledged fewer young than the 16 pairs on 100% food intake (15 vs 23). DDE effects were less than in other trials.

Table 6. Reproductive performance of doves in Trial 3 (food restriction at egg laying)

Food intake (%) and DDE	Egg laying		Eggs hatched		Young fledged		Performance index[a]
	No. pairs	No. eggs	No. eggs	%	No. young	%	
100							(a)
None	8	16	12	75	12	100	55.6 4.4
DDE	8	14	12	86	11	92	48.4 6.3
90							(ab)
None	8	16	13	81	6	46	48.9 6.3
DDE	8	15	9	60	5	56	41.0 4.6
80							(bc)
None	8	16	10	63	3	30	38.5 6.4
DDE	8	16	10	63	1	10	38.1 3.3
70							(c)
None	8	16	6	38	0	0	28.5 3.5
DDE	8	15	2	13	0	0	24.6 3.4

[a]Data are $\bar{x}$ and SE for eight pairs. $P < 0.001$ for food effects; there were no significant DDE effects or interactions

Condition Trial 6 was terminated at 30 days after pairing to enable evaluation of adult condition during the period that greatest nesting failure occurred in Performance Trial 3. Two pairs in the X-70 group failed to lay eggs before the termination of Trial 6 and were never subjected to food restriction. Data on those pairs were omitted from all summaries and calculations. The number of eggs that hatched and the number of young alive after 30 days were similar for the same treatment groups in Trials 3 and 6. This was illustrated by the lack of difference ($P = 0.724$) between performance indices accumulated by treatment groups in the two trials after 30 days. At termination of Trial 6, performance indices were similar for groups at all food intake levels. This occurred because most pairs had successfully maintained their eggs and young until shortly before they were sacrificed. Clean pairs (33.2) had higher performance indices ($P = 0.073$) than DDE pairs (27.6); the difference probably was due to a delay in egg laying in the DDE females.

Testes in the 100 and 90% food groups (Table 7) were about normal in weight for males with young. In contrast, testes in the 80 and 70% groups were significantly lighter ($P < 0.001$). No effects of DDE were evident on the weight of testes. Ovary weights in the 100, 90, and 80% intake groups (Table 7) were about normal for females with young, but ovaries of females on 70% food intake were as light as inactive females (0.16 g) and lighter ($P = 0.066$) than the 100 group. Ovary weights were not influenced by DDE. Weights of oviducts seemed to decrease with increased food restriction, but this trend was not significant (Table 7). DDE did not affect oviduct weights.

In Trial 6, crop glands from all birds were excised and weighed. There were no real differences in crop weights due to either DDE or the sex of the birds, but crop weights differed considerably ($P < 0.001$) with the level of food intake (Table 8). Average crop weights were 4.99, 4.31, 3.30, and 2.12 g for the 100, 90, 80, and 70% intake groups, respectively. For several weeks, young birds are largely dependent upon secretions from an active, fully developed crop for their food. At the termination of Trial 6, the 60 young alive ranged in age from 1 to 8 days. Adults in the 100, 90, 80, and 70% food groups had 22, 17, 13, and 8 young, respectively. These young were weighed at termination. The weight of each, less 8 g to compensate for normal weight at hatching, was divided by its age in days to obtain a figure for weight gain per day. Average daily

Table 7. Average measurements of gonads and oviducts for doves in Trial 6 (food restricted at egg laying and trial terminated 30 days after pairing)[a]

Food intake (%) and DDE	Testis weight (g)		Ovary weight (g)		Oviduct weight (g)	
100	(a)		(a)			
None	0.62	0.05	0.28	0.02	0.43	0.07
DDE	0.57	0.06	0.33	0.02	0.45	0.09
90	(a)		(ab)			
None	0.46	0.04	0.25	0.02	0.30	0.04
DDE	0.49	0.05	0.27	0.04	0.32	0.03
80	(b)		(ab)			
None	0.22	0.07	0.30	0.16	0.65	0.40
DDE	0.30	0.02	0.22	0.02	0.18	0.01
70	(b)		(b)			
None	0.21	0.04	0.14	0.01	0.20	0.02
DDE	0.24	0.06	0.13	0.02	0.25	0.06

[a]Data are $\bar{x}$ and SE for eight pairs, except X-70 where $n = 6$. Food effects were significant for testis weight ($P < 0.001$) and ovary weight ($P = 0.066$). There were no significant DDE effects or interactions

gains for young in the 100, 90, 80, and 70% groups were 7.8, 7.9, 3.7, and 3.0 g, respectively. Weights of young in the 80 and 70% food groups were significantly less ($P < 0.001$) than those of young in the 90 and 100% groups and showed the effects on young of the reduced crop weights in parents on 80 and 70% food intake. It appeared that once crop weights dropped below about 4.0 g, young received inadequate food and did not achieve normal weight gains.

Weights of adults were recorded eight times during Trial 6. Analysis of weight data showed interactions between dates and each of the main factors of DDE, food intake, and sex. As in other trials, DDE birds often weighed less ($P < 0.001$) than clean birds, but at the end of the trial the average weights of the two groups were similar. Doves on different levels of food intake differed in mean body weight only at termination of the trial. Average body weights then were significantly lower ($P < 0.001$) at each more severe level of food restriction (156, SE 2.4; 150, SE 3.3; 145, SE 3.1; and 136, SE 1.9 g; at the 100,

Table 8. Average weights of crops and breast muscle for doves in Trial 6 (food restricted at egg laying and trial terminated 30 days after pairing)[a]

Food intake (%) and DDE	Weight of crops: Males (g)		Weight of crops: Females (g)		Weight of breast muscle: Males (g)		Weight of breast muscle: Females (g)	
100	(a)				(a)			
None	4.41	0.64	5.40	0.95	16.0	0.6	15.0	0.6
DDE	4.85	0.34	5.30	0.38	15.8	0.6	14.5	0.4
90	(ab)				(ab)			
None	4.73	0.47	2.12	0.69	16.2	0.8	13.4	0.6
DDE	3.68	0.76	3.73	0.65	14.5	0.4	13.6	0.2
80	(bc)				(bc)			
None	3.73	0.82	2.46	0.38	14.4	0.4	13.7	0.4
DDE	3.38	0.44	3.62	0.58	14.4	0.6	12.8	0.6
70	(c)				(c)			
None	2.50	0.36	2.04	0.33	13.3	0.5	12.2	0.5
DDE	2.15	0.26	1.71	0.30	13.9	0.7	12.0	0.6

[a]Data are $\bar{x}$ and SE for eight pairs, except for X-70 where n = 6. Food effects were significant ($P < 0.001$) for both crop weights and breast muscle weights; sex effects only for breast muscle weights ($P < 0.001$). There were no significant DDE effects or interactions

90, 80, and 70% food levels, respectively). Food restriction apparently stressed females more than males. Both sexes weighed about 148 g at food restriction, but changes during the following 3 weeks were significant ($P < 0.001$); females lost an average of 12 g while males gained 4 g. (A separate test was conducted with 10 pairs subjected to 20% food restriction for 3 weeks. Based on weights taken before and after feeding, neither sex was consistently able to obtain more of the limited rations than the other.)

Weights of breast muscle followed trends established by body weights and decreased at each level of increasing food restriction (Table 8). Average weights of breast muscle were 15.3, 14.4, 13.9, and 12.9 g for the 100, 90, 80, and 70% groups, and breast muscle constituted 9.8, 9.6, 9.6, and 9.4% of the average body weight of each group, respectively. Breast muscle accounted for about the same percentage of body weight at each food intake level, and this was true for both sexes, suggesting that loss of body weight was largely due to loss of muscle tissue, since there were no treatment effects on either carcass or adipose lipids. Average lipid content of carcasses was lower ($P < 0.001$) in females (7.5%) than in males (9.2%), but there were no sex differences in the lipid content of adipose tissue (males 57%, females 53%).

As in other trials, DDE residues in carcasses and in adipose tissue varied widely among individuals, and no real differences were present between averages for sex or for levels of food intake. Residue levels were lower in Trial 6 than in other trials. Carcass residues in DDE birds averaged 74.7, SE 10.0 ppm in Trial 4; 70.8, SE 10.2 ppm in Trial 5; but only 46.5, SE 5.8 ppm in Trial 6. Similarly, DDE residues in adipose tissue were 592, SE 74 ppm in Trial 4; 547, SE 92 ppm in Trial 5; and 393, SE 59 ppm in Trial 6.

In Trial 6, as in Trial 3, food restrictions severely limited the nesting success of doves, but, in contrast to other trials, the effects of DDE were less obvious. Losses of eggs and young became progressively greater with increased food restriction.

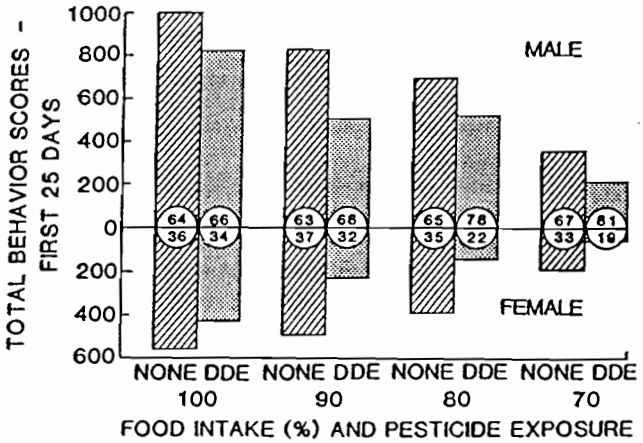

Fig. 2. Total behavior scores by sex and treatment groups during the first 25 days of Trial 2 (food restriction at pairing). Percentage of behavior by males and females shown in circles

Those losses were accompanied by a decrease in weights of gonads, oviducts, crops, breast muscle, and carcasses. Any or all of the latter features could have been causally related to reproductive failure; the pattern of change in their values at different levels of food restriction paralleled those for reproductive debility.

Relative Treatment Effects on Males and Females

Behavior data for the first 25 days of Trial 2 were compiled by sex to assess if there were differences in treatment effects on male and female behavior. Trial 2 gave the most complete coverage of behavior during courtship and incubation under the influence of food restrictions. Daily scores were totaled for males and females in each treatment group for the 25-day period (Figure 2). Scores for both sexes decreased with increased food restriction ($P < 0.001$). At each food intake level, DDE birds of both sexes had considerably lower scores than clean birds ($P < 0.001$) and were less than the clean birds at the next lower level of food intake.

Most behavior was displayed by males; overall males accounted for 67% of the score values. In clean birds, the proportion of behavior displayed by males and females remained relatively constant in the different food treatment groups. In contrast, DDE males accounted for an increasingly greater percentage of the behavior as food intake decreased. Whereas clean males displayed about 65% of the behavior at all food levels, DDE males increased their proportion of the behavior from 66% at 100% food intake to 81% at the 70% level; it appeared that DDE females were more affected by food restrictions than DDE males, but this was not true in clean birds. In Trial 2, DDE pairs were less successful than clean pairs (Table 4). The decreased performance of DDE pairs may have been related to a failing in behavioral participation by females.

In doves, both sexes incubate and brood young. The participation by each sex in nesting duties was evaluated in relation to nesting success in Trial 3. Trial 3 was chosen for this assessment because all pairs had laid eggs before food treatments were imposed. Each weekday, records of which sex was on the nest were taken once in the morning (0800-0900 h) and once in

Table 9. Relative occupancy of nests by males and females related to time of day and nesting success for Trial 3[a]

Nesting period and time of day	Successful nests		Failing nests	
	Males on	Females on	Males on	Females on
Incubation period				
AM	2.6	7.6	3.3	3.7
PM	7.0	2.4	5.1	1.0
Care of young period				
AM	2.0	5.1	0.5	0.8
PM	4.3	1.3	0.7	0.4

[a]Data are average numbers of times each sex was observed on the nest (one observation in the morning and one in the afternoon each day; maximum of 11 days during incubation and 15 days during care of young periods)

the afternoon (1630-1700 h) for pairs in all treatment groups. Observations on individual nests were obtained for a maximum of 11 days during incubation and 15 days during care of young. On occasion, neither parent was on the nest when an observation was made.

For successful nests in which eggs hatched, females tended to incubate in the morning and males in the afternoon (Table 9). In nests where eggs failed to hatch, females were on nests in the morning only about half as often. Male participation in morning incubation increased slightly in those cases, but sometimes neither bird was on the nest. In the afternoon, the incidence of male incubation was higher in nests in which eggs hatched than in failing nests. However, female participation also decreased in failing nests, and often neither bird incubated. Results suggested that eggs failed to hatch because of inattention by adults and that females were less dependable than males in maintaining incubation duties.

Similarly, during care of young, females tended to be on nests in the morning and males in the afternoon (Table 9). Birds that lost their young were seldom on nests in either the morning or afternoon. Nests of the 100% food groups all fledged young and were usually covered both in the morning and afternoon. However, even the successful pairs on restricted food intakes brooded less frequently. This finding suggested that continuous brooding was not essential to raising young (at least under conditions where ambient temperatures were adequate and constant) and that losses of young were related more to amounts of food they received from adults (see crop weights, Table 8, and related text).

Factors Influencing Performance and Productivity

In all trials, females with DDE residues tended to take longer to lay their first egg. To test these results, data from Trials 2 and 3 were subjected to three-way analysis of variance for food intake, DDE, and trials. Because many birds in Trial 1 did not lay eggs, results from that trial were not used. Only females that laid within the first 3 weeks were included in the analysis. This eliminated an unusual and prolonged delay (23–37 days) by five DDE females in Trials 2 and 3. Females with DDE residues took longer ($P = 0.001$) by an average of more than 3 days to lay their eggs.

Food restrictions did not influence clutch size; at all food levels, if females laid, they rather consistently produced two eggs. The six single-egg clutches laid during the three trials were all produced by DDE females (Tables 2, 4, and 6). Apparently, DDE had the effect of reducing clutch size in a few females.

The experimental design provided for an evaluation of DDE effects on eggshell thinning. However, sufficient eggs and eggshell fragments for an assessment were available only in Trial 3. Because food restrictions were not imposed until after egg laying, lack of food could not have affected shell thickness in Trial 3. Shells of eggs laid by 10 DDE females were 1.3% thinner than shells of eggs laid by 18 clean females.

In Trials 1 and 2, food was restricted before females laid eggs. Treatments inhibited the initiation of reproduction, and many females did not lay. Of the 48 pairs on food restriction in each of those trials, only five females laid eggs in Trial 1, and only 23 females laid in Trial 2. Lack of egg production was the factor most responsible for poor reproductive success in Trials 1 and 2.

Some of the circumstances surrounding loss of eggs and young were noted during trials. A few eggs were infertile (10); embryos in others died during incubation (69), often after parental neglect and nest desertion. Infertile eggs and those with dead embryos were left in nests. Often adults on food restriction partly ate the shells and contents of the inviable eggs (24 incidences). Some eggs disappeared and were assumed to have been entirely consumed. Egg eating usually followed nesting failure and was not itself a cause of failure. Many young died during trials (56); most such deaths apparently were the result of inadequate care by adults.

Importance of Timing of Food Restriction

Performance indices from all three trials were combined and subjected to a three-way analysis of variance to assess overall performance as influenced by DDE, levels of food restriction, and especially timing of food restriction. Performance indices decreased as food intake decreased ($P < 0.001$), were lower in pairs with DDE residues ($P < 0.001$), and increased when the later food restrictions were imposed ($P < 0.001$). Significant interactions also were found between all of the main treatments. DDE birds consistently performed more poorly than clean birds ($P < 0.001$) at the 100, 90, and 80% food intake levels (Figure 3A). The depressing effect of DDE on performance of birds on 100% food was comparable to a 10% food reduction in clean birds. The greatest effect of DDE was seen on birds subjected to a minor food shortage; in the 90% groups, DDE reduced the average performance index by almost two-thirds. At the 70% level, performance was drastically reduced regardless of DDE treatments.

Performance of birds at different food intake levels varied with the time food restrictions were imposed (Figure 3B). Food restrictions at and before pairing had much greater effects at all intake levels than food restriction at egg laying ($P < 0.001$). Food restriction before pairing precluded successful performance in almost all birds. A 10% reduction in food before pairing had a greater effect on performance indices than a 30% reduction in egg laying. Therefore, the timing of food restriction was as important as the level of restriction in influencing performance. The timing of food restriction also influenced the effect of DDE on performance ($P < 0.001$; Figure 3C). The effects of DDE appeared greater when food was restricted at

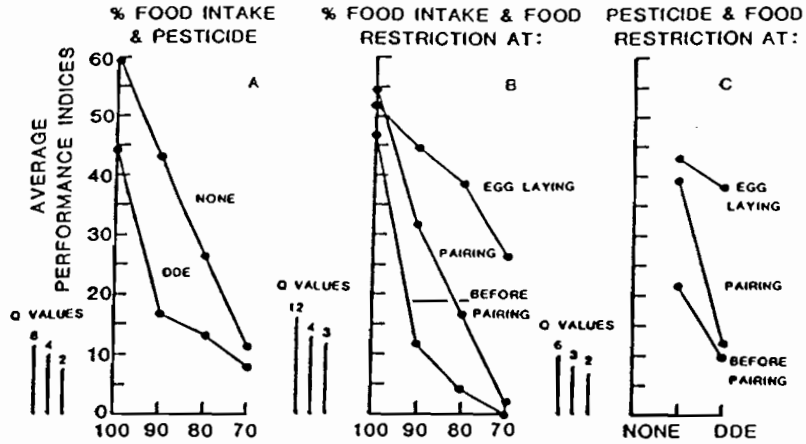

Fig. 3. Effects of the interaction of food intake, DDE, and timing of food restrictions on performance indices (means and Q values) averaged over the three performance trials. In Figure 3A, for example, there are eight means. Q values for Figure 3A show units between any two (food intake), four (pesticide), or eight (interaction) means that are significantly different

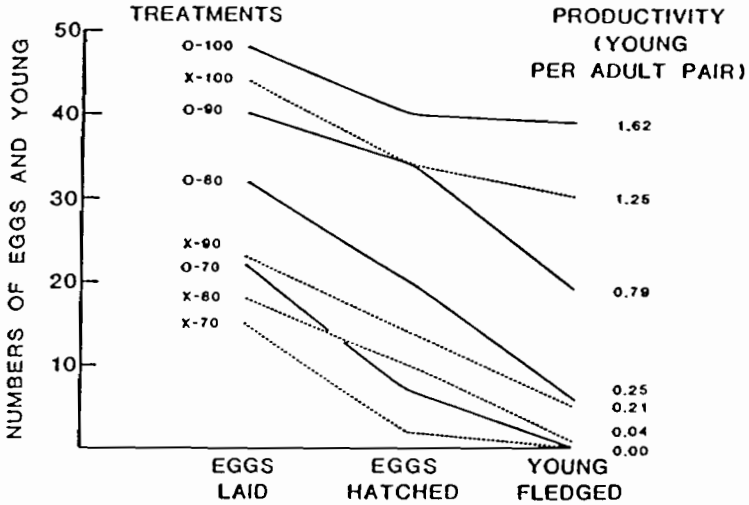

Fig. 4. Average productivity, by treatment groups, in the three performance trials

pairing than when food was restricted before pairing or at egg laying. The timing of food restriction completely altered the impact of DDE on birds.

The results of these comparisons illustrate the complexity of interactions between DDE, food levels, and the timing of food deprivation. Each factor can have major effects, which can be modified by variation in the other factors.

Productivity in Performance Trials

Nesting success and ultimate productivity (young per adult pair) of treatment groups were averaged across all performance trials (Figure 4). This was done to help summarize trial results and to simulate reproductive effects on avian predators carrying DDE residues and confronted with periodic food shortages before and during their reproductive period.

Increased food restrictions progressively reduced nesting success and productivity in clean birds. Compared to controls (0-100), productivity was reduced about 50, 85, and 100% in the 0-90, 0-80, and 0-70 groups. DDE reduced productivity even without food restriction. Productivity was reduced 23%, from 1.62 young per adult pair in the 0-100 groups to 1.25 in the X-100 groups. Other groups exposed to DDE (X-90, X-80, and X-70) showed much lower productivity than clean groups at all food restriction levels. Clearly, productivity was depressed by both food restriction and DDE, and effects were synergistic. For instance, DDE alone reduced productivity 23% (0-100 vs X-100). A 10% food restriction reduced productivity 50% (0-100 vs 0-90). However, the combination of DDE and a 10% food restriction lowered productivity 87% (0-100 vs X-90).

Discussion

Performance trials with doves demonstrated the effects on reproduction of different timings and intensities of food restriction, with and without the influence of DDE. Body burdens of DDE in doves on food restrictions primarily affected their ability to form pair bonds, mate, and produce eggs. Food restrictions influenced egg production, but also had pronounced effects on the ability of pairs with eggs to fledge young. The timing of food restrictions was important; a 10% reduction in food before pairing depressed performance indices more than a 30% reduction at egg laying. Behavior scores were good indicators of the effects on males and females of food restrictions and DDE. Behavior was a good predictor of impending problems in reproductive performance. Birds immediately reacted to food restrictions by decreasing behavioral displays. In Trial 2, doves on 70% intake ceased normal intensities of displays beginning the day after food was restricted. Only pairs with

substantial courtship behavior scores laid eggs. Those with continued high scores successfully hatched their eggs and reared their young. Decreasing behavior scores in birds with eggs or young signaled the collapse of their reproductive efforts. Evaluations of performance and behavior by sex showed that females were more seriously affected by treatments than males. In Trial 2, total scores for pairs decreased with food restriction, but males, and especially DDE males, tended to participate to a greater extent than females with each increase in food restriction. This evidence indicated that food restrictions greatly decreased behavior scores for pairs, but, in DDE pairs, females were more affected than males.

Condition trials suggested that failure in reproductive performance was more closely related to changes in gonads (Trials 4 and 5) and crop glands (Trial 6) than to any other characteristics measured. Gonad development is under hormonal control, and hormones secreted by the ovary induce nest building and incubation behavior in ringed turtle doves (Cheng and Silver 1975; Silver and Ball 1989). The high incidence of dead embryos in eggs indicated an inadequacy in incubation, while loss of young and reduced crop weights illustrated an inability of adults to produce adequate food for young. In doves, incubation is maintained by progesterone and crop development by prolactin (Silver 1978).

Most results indicated that food restrictions and DDE adversely influenced reproduction by reducing levels of circulating gonadotropins and sex steroids. These findings support current theory on the energetics of avian reproduction. In a review of reproductive energetics in birds, King (1973) concluded that the caloric status of birds is monitored by the hypothalamo-hypophyseal axis. Reproductive activities are adjusted to the level of energy intake through control of the secretion of gonadotropic hormones. The failure of pairs to lay eggs probably was the result of decreased gonadotropin secretion by the pituitary in response to restricted food intake and DDE. Luteinizing hormone, a gonadotropin, acts on the gonads to initiate androgen and estrogen secretion. Richie and Peterle (1979) showed that circulating levels of luteinizing hormone were reduced in doves exposed to DDE. The gonadotropins provide for maturation of the gonads and, thereby, the increased production of estrogens and androgens. Such stimulation is essential for egg production.

McArthur *et al.* (1983) studied reproductive behavior and performance in ringed turtle doves exposed in diet to a mixture of organochlorine compounds. Concurrently they measured circulating levels of androgens, estrogens, progesterone, prolactin, and thyroxine. Their findings provided a basis for understanding the hormonal response to organochlorine exposure and its effect on reproduction. Treatments reduced androgen and estrogen levels in plasma, which probably caused deficient early courtship behavior. Treatments reduced progesterone levels in females, and that may have created delays in nest building, ovulation, and incubation. Females were not as responsive to male courtship and participated less in nesting activities, all of which were related to lower levels of estrogen and progesterone than were present in control birds. The organochlorine diets resulted in increased thyroxine levels and decreased attentiveness to incubation and brooding. The authors concluded doves exposed to organochlorines were hyperactive due to high circulating levels of thyroxine and, thereby, less attentive to nesting duties.

Tori and Peterle (1983) produced both extended courtship periods and reduced behavior scores in mourning doves (*Zenaida macroura*) by feeding 40 ppm Aroclor® 1254 in diet before pairing for reproduction. They, too, found females to be more affected than males. In another study, Aroclor® 1254 fed to ringed turtle doves affected hatching success, primarily through behavioral debility of females (Peakall and Peakall 1973). Egg temperatures varied much more in treated than in control pairs, which suggested that lack of nesting attentiveness was responsible for the greatly increased embryo mortality. In the present study, nest occupancy was not influenced by DDE; at all levels of food restriction the occupancy of nests by DDE pairs was comparable to that of clean pairs.

Many other studies with a variety of species have evaluated the effects of DDT and DDE on avian reproduction (Stickel 1973; Peakall 1985). Several kinds of debilities were demonstrated in the species tested, including delayed ovulation, reduced fertility and egg production, eggshell thinning, embryo death, poor hatchability, and loss of young. In those studies, birds had adequate food and failed to breed only when levels of toxicant in diet were high enough to make birds sick.

Similarly, in the current study, DDE alone (X-100 groups) did not influence the number of pairs attempting to breed. Nonbreeding occurred only with food restriction, and then DDE residues in birds greatly aggravated the effects. In field studies, nonbreeding in adults has not often been reported, but it is a difficult parameter to quantify and an effect that might not be readily apparent. Nonbreeding should be expected, however, because food restrictions must sometimes occur in birds carrying DDE residues.

Abnormal nesting behavior has often been suggested as being responsible for reproductive failure in species exposed to DDE (Ratcliffe 1958, 1965; Cade *et al.* 1968; Snyder *et al.* 1973). However, little definitive information on such relationships under field conditions is available (Stickel 1973). At Lake Ontario, Canada, observations suggested that reproductive failure in herring gulls (*Larus argentatus*) was related partially to aberrant behavior in adults with high body burdens of organochlorines (Fox *et al.* 1975, 1978). Egg-exchange experiments demonstrated that gull eggs from Lake Ontario contained embryotoxic substances, but, in addition, behavioral deficiencies were implied in Lake Ontario gulls since they were not able to hatch normal eggs as successfully as gulls elsewhere with low pesticide residues. Neuroendocrine effects from high levels of organochlorine residues were suspected as the cause of behavioral debilities.

The knowledge that DDE interacts with food stress to depress the productivity of avian species creates a new dimension in assessing the hazards of DDT use. Although severely restricted in some countries, DDT use continues over much of the world. Residues remain at high levels in some resident North American birds, and especially in migratory species as a result of their continued exposure, or exposure of their prey, elsewhere in the hemisphere (Henny *et al.* 1984; DeWeese *et al.* 1986; Ellis *et al.* 1989; Henny and Herron 1989). DDT problems also occur in raptors on other continents (Douthwaite 1992). It must be assumed that food stress is often present in breeding birds. Avian populations have adapted to handle normal food stresses, but abnormal food scarcity caused by human activities and additional debilitation by DDE place them in double jeopardy. Thus, it is essential that management to preserve and protect wildlife consider the consequences of such interactions and strive to maintain adequate levels of food resources for animals while protecting their habitats from contamination with biologically active chemicals.

Acknowledgments. We thank Earl C. Schafer for providing much of the routine care of doves over the 5 years of this research. Most of the protocols and facilities for maintaining doves at our Center were developed by Max A. Haegele and Rick H. Hudson, and their advice and guidance were helpful. Marilyn Campion conducted most statistical analyses, and she and David L. Otis advised and assisted in selection of methods and interpretation of results. Typing and considerable improvement in style and grammar were accomplished by Anna E. Valvano and Marilyn A. Harris. The manuscript was reviewed by D. W. Anderson, G. A. Fox, R. L. Kirkpatrick, T. J. Peterle, and P. F. Scanlon. The valuable contributions of the above to this study are appreciated. The authors were assigned to the Patuxent Wildlife Research Center, U.S. Fish and Wildlife Service, during preparation of the original manuscript.

References

Brown AWA (1978) Ecology of pesticides. John Wiley and Sons, NY, 525 pp

Cade TJ, White CM, Haugh JR (1968) Peregrines and pesticides in Alaska. Condor 70:170–178

Cheng M-F, Silver R (1975) Estrogen-progesterone regulation of nest-building and incubation behavior in ovariectomized ring doves (*Streptopelia risoria*). J Comp Physiol Psychol 88:256–263

DeWeese LR, McEwen LC, Hensler GL, Peterson BE (1986) Organochlorine contaminants in Passeriformes and other avian prey of the peregrine falcon in the western United States. Environ Toxicol Chem 5:675–693

Douthwaite RJ (1992) Effects of DDT on the fish eagle *Haliaeetus vocifer* population of Lake Kariba in Zimbabwe. Ibis 134:250–258

Ellis DH, DeWeese LR, Grubb TG, Kiff LF, Smith DG, Jarman WM, Peakall DB (1989) Pesticide residues in Arizona peregrine falcon eggs and prey. Bull Environ Contam Toxicol 42:57–64

Fox GA, Gilman AP, Hallett DJ, Norstrom RJ, Onuska FI, Peakall DB (1975) Herring gull productivity and toxic chemicals in the Great Lakes in 1975. Toxic Chemicals Division, Can Wildl Serv, Ottawa, Manuscript Rep 34, 35 pp

———, ———, Peakall DB, Anderka FW (1978) Behavior abnormalities of nesting Lake Ontario herring gulls. J Wildl Manage 42:477–483

Henny CJ, Blus LJ, Krynitsky AJ, Bunck CM (1984) Current impact of DDE on black-crowned night-herons in the intermountain west. J Wildl Manage 48:1–13

———, Herron GB (1989) DDE, selenium, mercury, and white-faced ibis reproduction at Carson Lake, Nevada. J Wildl Manage 53:1032–1045

Hickey JJ, Anderson DW (1968) Chlorinated hydrocarbons and eggshell changes in raptorial and fish-eating birds. Science 162:271–273

Keith JO (1978) Synergistic effects of DDE and food stress on reproduction in brown pelicans and ringdoves. PhD Dissertation. Ohio State University, Columbus OH, 185 pp

King JR (1973) Energetics of reproduction in birds. In: Farner DS (ed) Breeding biology of birds. National Academy of Sciences, Washington, DC, pp 78–107

Lehrman DS (1965) Interaction between internal and external environments in the regulation of the reproductive cycle of the ring dove. In: Beach FA (ed) Sex and behavior. John Wiley & Sons, NY, pp 355–380

———, Wortis RP (1967) Breeding experience and breeding efficiency in the ring dove. Anim Behav 15:223–228

McArthur MLB, Fox GA, Peakall DB, Philogène BJR (1983) Ecological significance of behavioral and hormonal abnormalities in breeding ring doves fed an organochlorine chemical mixture. Arch Environ Contam Toxicol 12:343–353

Miller WJ, Miller LS (1958) Synopsis of behaviour traits of the ring neck dove. Anim Behav 6:3–8

Peakall DB (1970) Pesticides and the reproduction of birds. Sci Am 222:73–78

———(1985) Behavioral responses of birds to pesticides and other contaminants. Pesticide Rev 96:45–77

———, Peakall ML (1973) Effect of a polychlorinated biphenyl on the reproduction of artificially and naturally incubated dove eggs. J Appl Ecol 10:863–868

Peterle TJ (1991) Wildlife toxicology. Van Nostrand and Reinhold, NY, 322 pp

Ratcliffe DA (1958) Broken eggs in peregine eyries. Br Birds 51:23–26

———(1965) The peregrine situation in Great Britain 1963–64. Bird Study 12:66–82

Richie PJ, Peterle TJ (1979) Effect of DDE on circulating luteinizing hormone levels in ring doves during courtship and nesting. Bull Environ Contam Toxicol 23:220–226

Silver R (1978) The parental behavior of ring doves. Am Sci 66:209–215

Silver R, Ball GF (1989) Brain, hormone and behavior interactions in avian reproduction: status and prospectus. Condor 91:966–978

Smith GJ (1987) Pesticide use and toxicology in relation to wildlife: organophosphate and carbamate compounds. US Fish Wildl Serv Resour Publ 170. 171 pp

Snyder NFR, Snyder HA, Lincer JL, Reynolds RT (1973) Organochlorines, heavy metals, and the biology of North American accipiters. Bioscience 23:300–305

Steel R, Torrie J (1960) Principles and procedures of statistics. McGraw- Hill, NY, 481 pp

Stickel L (1973) Pesticide residues in birds and mammals. In: Edwards CA (ed) Environmental pollution by pesticides. Plenum Press, London, pp 254–312

Tori GM, Peterle TJ (1983) Effects of PCBs on mourning dove courtship behavior. Bull Environ Contam Toxicol 30:44–49

Manuscript received December 12, 1992 and in revised form March 1, 1993.

Wildlife Research Center Library
90016917