NEST SUCCESS, CAUSE-SPECIFIC NEST FAILURE, AND HATCHABILITY OF AQUATIC BIRDS AT SELENIUM-CONTAMINATED KESTERSON RESERVOIR AND A REFERENCE SITE[1]

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Abstract. During 1983–1985, we studied the reproductive success of several species of aquatic birds (coots, ducks, shorebirds, and grebes) nesting at two sites in Merced County, California: a selenium-contaminated site (Kesterson Reservoir) and a nearby reference site (Volta Wildlife Area). We used a computer program (MICROMORT) developed for the analysis of radiotelemetry data (Heisey and Fuller 1985) to estimate nest success and cause-specific failure rates, and then compared these parameters and hatchability between sites and among years.

Nest success and causes of failure varied by species, site, and year. The most important causes of nest failure were usually predation, desertion, and water-level changes. However, embryotoxicosis (mortality, deformity, and lack of embryonic development) was the most important cause of nest failure in Eared Grebes (*Podiceps nigricollis*) at Kesterson Reservoir. Embryotoxicosis also reduced the hatchability of eggs of all other species at Kesterson in one or more years; embryonic mortality occurred rarely at Volta, and abnormalities were not observed.

Key words: Reproductive success; nest failure; embryotoxicosis; hatchability; Kesterson Reservoir; selenium; California.

INTRODUCTION

Selenium is an essential trace element that, at elevated dietary levels, has been found to impair reproduction in birds (Ort and Latshaw 1978, Eisler 1985, Heinz et al. 1987, Ohlendorf 1989). High rates of embryonic mortality and deformity attributable to the adverse effects of selenium were observed in most species studied at Kesterson Reservoir (Ohlendorf et al. 1986a, 1986b). However, other causes of nesting failure at both Kesterson and the reference site complicated evaluation of the impacts of selenium on nesting success.

The Mayfield method, which estimates nest success based on days of exposure of sampled nests, provides statistically testable estimates that are less biased than those obtained using traditional methods (Mayfield 1961, Hensler and Nichols 1981). A computer program (MICROMORT) that calculates Mayfield method estimates of nest success, and also produces estimates of cause-specific mortality rates, is available (Heisey and Fuller 1985). Although developed

for analysis of radiotelemetry data, MICROMORT is applicable to the study of cause-specific nest failure, but has rarely been used for this purpose.

In addition to causing complete failure of some nests, selenium often caused mortality of one or more eggs in otherwise successful nests (Ohlendorf et al. 1986b). Cause-specific nest failure estimates do not address the problem of partial losses. By quantifying partial losses, estimates of hatchability complement estimates of cause-specific nest failure. In uncontaminated populations of aquatic birds, hatchability ("the proportion of eggs surviving to the end of incubation that hatch") averages about 91% (Koenig 1982).

The objective of this paper is to compare nest success, cause-specific nest failure, and hatchability rates of aquatic birds at Kesterson Reservoir and an uncontaminated reference site.

METHODS

STUDY AREAS

Our primary study area was Kesterson Reservoir (hereafter called Kesterson), located on the Kesterson National Wildlife Refuge, about 8 km east of Gustine and 16 km north of Los Banos, Merced
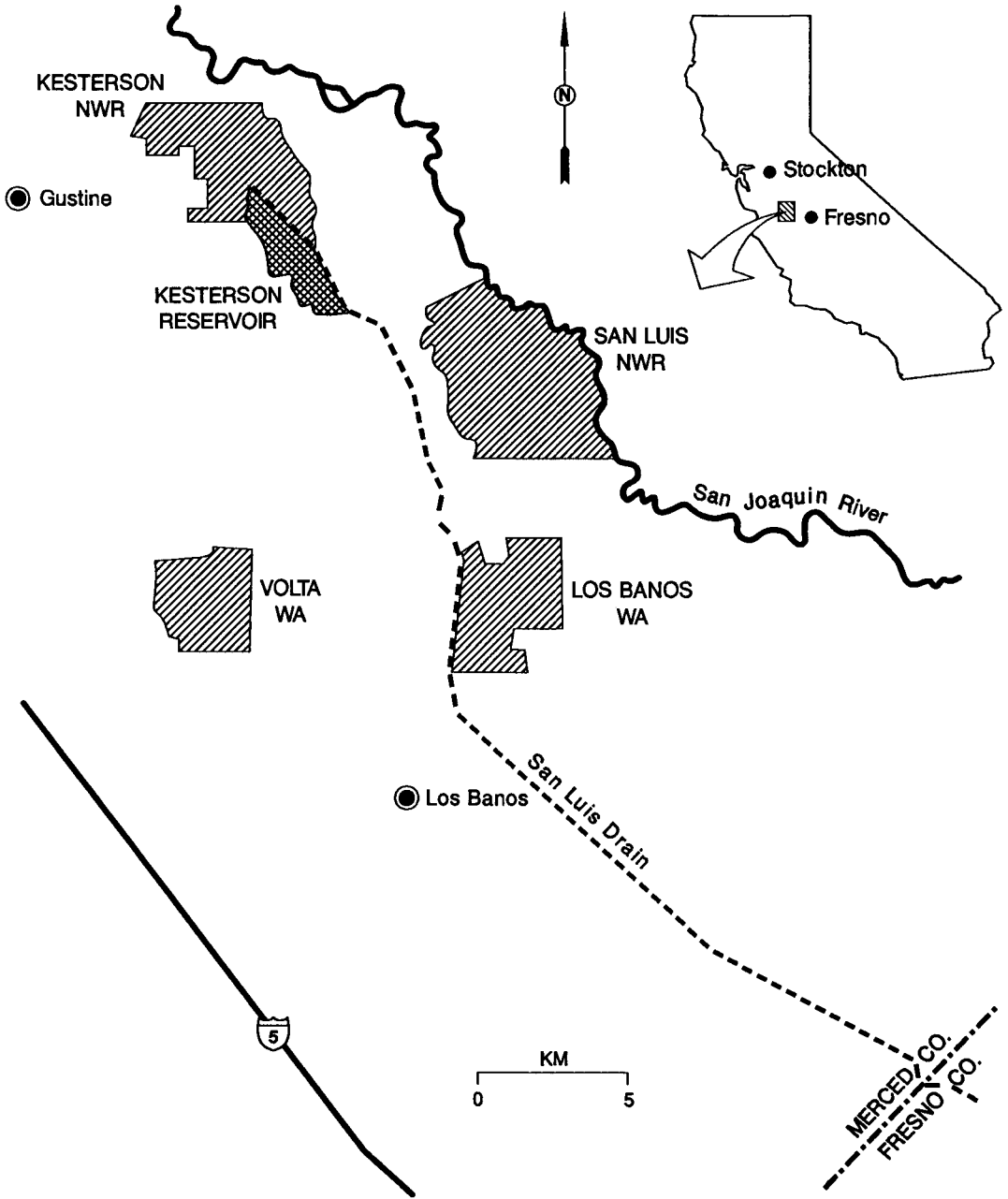
FIGURE 1.   Map showing the locations of study sites (Kesterson Reservoir and Volta Wildlife Area) in western Merced County, California.

County, California (Fig. 1). During our study, Kesterson's water source was subsurface agricultural drain water from fields in Fresno County. In 1983, this water contained elevated (300 μg/l) levels of selenium (Presser and Ohlendorf 1987, Saiki and Lowe 1987). Aquatic birds nested in grasslands, emergent vegetation, and alkali flats present at Kesterson. For a more detailed description of the study area, see Ohlendorf et al. (1986b).

The reference area for our study was the Volta Wildlife Area (Fig. 1), located about 10 km southwest of Kesterson (Ohlendorf et al. 1986b). This state-managed area received water that was not contaminated by selenium-laden agricultural drain water (Saiki and Lowe 1987). Nesting habitat of aquatic birds at Volta was otherwise qualitatively similar to that at Kesterson.

FIELD AND LABORATORY METHODS

Each week during April–June 1983–1985, likely nesting habitats at Kesterson and Volta were searched on foot for active nests of aquatic birds. The following species were studied: Eared Grebe (*Podiceps nigricollis*), Mallard (*Anas platyrhynchos*), Cinnamon Teal (*Anas cyanoptera*), Gadwall (*Anas strepera*), American Coot (*Fulica americana*), Killdeer (*Charadrius vociferus*), Black-necked Stilt (*Himantopus mexicanus*), and American Avocet (*Recurvirostra americana*). Nests were marked with flags and visited weekly to monitor the incubation status of eggs and to determine nest fates.

Eggs were collected to assess the relationship between reproductive success and selenium concentrations, which are described elsewhere (Ohlendorf et al. 1986b, unpubl.). Random eggs were those collected from each nest in a randomly selected subgroup of marked nests. Nonrandom eggs were those that failed to hatch or were collected for other reasons. Random collections were generally made early in incubation before it was possible to assess embryo normality, whereas nonrandom collections were generally made to determine normality of late-stage embryos or embryos in eggs that failed to hatch.

The combined lengths of the egg-laying and incubation periods of the species included in this study varied from 21–35 days (Table 1). All species were assumed to lay one egg per day. Incubation was assumed to begin upon clutch initiation by Eared Grebes (Palmer 1962), upon laying of the second egg by coots (Heaslip 1981), and upon clutch completion by Killdeer (Nol and Lambert 1984) and ducks (Klett et al. 1986). Because nesting-period lengths of stilts and avocets were based on nests found with incomplete clutches and visited on hatching dates, no assumptions about the extent of overlap of egg-laying and incubation periods were necessary.

Ages of nests found with incomplete clutches were determined by back dating, assuming that one egg was laid per day. Incubation stages of

TABLE 1. Lengths of nesting intervals of aquatic birds.

Species	Interval length[a]	Reference
Eared Grebe	21	Palmer 1962
Mallard	35	Klett et al. 1986
Cinnamon Teal	34	Johnsgard 1978
Gadwall	35	Klett et al. 1986
American Coot	24	Heaslip 1981
Killdeer	29	Nol and Lambert 1984
Black-necked Stilt	25	W. L. Hohman and H. M. Ohlendorf, unpubl. data
American Avocet	26	Hohman and Ohlendorf, unpubl. data

[a] Days between date first egg laid and date first egg hatched.

eggs in nests found with complete clutches were estimated by egg flotation (Westerskov 1950), candling (Weller 1956), or embryo examination (Caldwell and Snart 1974), enabling prediction of hatching dates (Klett et al. 1986). Evidence of hatching included the presence of nestlings or detached eggshell membranes in the nests. Eggs were presumed to have hatched if they disappeared from the nest during the week that they were expected to hatch and there were no indications of predation or other causes of nest failure.

In nests that were successful, we considered that nonrandomly collected eggs containing live, normal (undeformed) embryos older than 13 days (the minimum age at which we were confident in our ability to recognize gross external deformities) would have hatched. Recent work has confirmed that once eggs reach about half-way in incubation (i.e., 13 days) it is highly probable that they will hatch (J. P. Skorupa, pers. comm.). In that work, freshly laid stilt and avocet eggs were collected from nesting areas contaminated with selenium and were incubated in a hatchery. Although less than 75% hatched, the conditional probability of hatching, given that an egg collected from a successful nest contained a live normal embryo at day 13, was >95%. Thus our assumption that nonrandomly collected eggs were successful imparts minimal bias to our hatchability estimates, at least for stilts and avocets. It is more likely that this assumption would be violated at Kesterson than at Volta (due to selenium-induced embryotoxicosis). If so, hatchability would be overestimated at Kesterson, which would reduce (rather than increase) the

probability of detecting between-location differences in hatchability (i.e., our assumptions are conservative).

CAUSES OF NEST AND EGG FAILURE

Nests were considered unsuccessful only if all eggs failed to hatch (Mayfield 1975). Although eggs within a clutch were sometimes affected by several causes of failure, the event that finally terminated the nesting effort was considered the cause of nest failure. Within successful nests we determined causes of failure of individual eggs. Causes of nest and egg failure included predation, desertion, water-level changes, and embryotoxicosis.

Evidence of predation included yolk or partially eaten eggs in nests, or disappearance of eggs from nests before expected hatching dates. Nests were considered deserted if: (1) incomplete clutches were not completed, (2) there were no increases in the developmental stages of embryos on subsequent visits, or (3) eggs were cold and the nests appeared untended. Failures related to changes in water level included flooding of ground nests and the stranding of coot and grebe nests when water levels dropped. In nests that were not deserted, embryotoxicosis was the assumed cause of failure of eggs containing dead or deformed embryos and eggs with no discernible embryonic development. Since most eggs with no embryonic development were rotten, it was impossible to determine their fertility. Therefore, some infertile eggs may be included in the embryotoxicosis category.

DATA ANALYSIS

Rates of nest success and cause-specific nest failure (and associated 95% confidence intervals) were calculated using the computer program MICROMORT (Heisey and Fuller 1985). Data required by MICROMORT are: (1) length of the interval for which rates are to be calculated, (2) number of nests succumbing to each cause of failure during the specified interval, and (3) number of exposure days of nests in the sample during the specified interval.

The interval length we specified was the nesting interval (Table 1) because estimates obtained using this interval are estimates of rates of nest success and cause-specific nest failure. Nests of unknown fate, nests already terminated when found, and nests deserted on the day of the first visit were not included in analyses. Methods of calculating exposure days followed Johnson (1979) and Klett et al. (1986).

Between-year and between-location comparisons of success rates were made with two-tailed z-tests (Hensler and Nichols 1981, Bart and Robson 1982). Because estimates of cause-specific failure rates obtained with MICROMORT are nearly normally distributed (Heisey and Fuller 1985) we used z-tests to compare cause-specific failure rates. The probability level used to determine statistical significance for all tests was $P \leq 0.05$.

To assess hatchability (egg success), the ratio of hatched eggs to adjusted clutch size (see below) was calculated for each successful nest. For species in which embryotoxicosis was a cause of nest failure, hatchability was also calculated for nests that survived to predicted hatching dates. Following arcsine transformation, hatchability data were statistically compared using two-factor analysis of variance (ANOVA) and, if necessary, Bonferroni mean separation tests (Neter and Wasserman 1974).

Adjusted clutch sizes were calculated by subtracting from full clutch sizes all randomly collected eggs and eggs that disappeared from nests prior to predicted hatching dates. Some nonrandomly collected eggs contained live embryos younger than 13 days, and in some cases it was not possible to determine whether advanced embryos in nonrandomly collected eggs were alive or dead; nests from which these types of eggs were collected were rejected from analyses of hatchability. By adjusting clutch sizes and sample sizes in this manner, all causes of egg failure other than embryotoxicosis were eliminated; thus percent egg loss due to embryotoxicosis is equal to (100 − percent hatchability).

RESULTS

EARED GREBES

Eared Grebes nested only at Kesterson and only in 1983 (Table 2). At least one egg hatched in 72.6% of the nests (Table 3), with 59% of the nest failures attributable to embryotoxicosis (Table 4). In successful nests, nearly one-third of the eggs, including 11 that contained deformed embryos, failed to hatch due to embryotoxicosis (Table 5). Mean hatchability in successful nests was only 70%. When nests that failed due to embryotoxicosis were combined with the successful nests, hatchability was only 58%.

TABLE 2.   Numbers of nests of aquatic birds and their fates at Kesterson Reservoir (KR) and Volta Wildlife Area (VWA), 1983–1985.

Species and year(s)	Site	Found	Included[a]	Hatched[b]	Preda-tion	Deser-tion	Water level	Embryo-toxicosis	Unknown	Total failed	Exposure days
					Cause-specific failure categories						
Eared Grebe											
1983	KR	163	154	115	6	0	8	23	2	39	2,573.5
Mallard											
1983–1985	KR	40	37	21	14	1	0	1	0	16	404.0
1983–1985	VWA	10	7	3	4	0	0	0	0	4	78.0
Cinnamon Teal											
1983–1985	KR	17	14	5	8	0	0	0	1	9	120.5
1983–1985	VWA	6	5	2	2	1	0	0	0	3	65.0
Gadwall											
1983–1985	KR	33	30	12	13	4	0	1	0	18	436.0
1983–1985	VWA	7	6	0	6	0	0	0	0	6	54.5
American Coot											
1983	KR	92	73	53	7	1	8	3	1	20	888.5
1984	VWA	5	5	1	4	0	0	0	0	4	35.5
Killdeer											
1984–1985	KR	59	39	17	21	0	0	0	1	22	371.0
1984–1985	VWA	8	6	1	5	0	0	0	0	5	45.5
Black-necked Stilt											
1983	KR	125	112	94	4	0	8	2	4	18	1,494.5
1983	VWA	11	11	7	4	0	0	0	0	4	132.0
1984	KR	189	180	49	123	4	0	2	2	131	1,328.5
1984	VWA	31	30	5	13	0	12	0	0	25	302.5
1985	KR	96	82	47	30	4	0	1	0	35	843.0
1985	VWA	48	44	11	32	0	1	0	0	33	397.0
American Avocet											
1983	KR	17	17	16	0	0	1	0	0	1	190.5
1983	VWA	10	10	8	2	0	0	0	0	2	133.5
1984	KR	51	49	17	30	2	0	0	0	32	472.5
1984	VWA	62	58	24	22	1	10	0	1	34	548.5
1985	KR	35	34	19	14	1	0	0	0	15	344.5
1985	VWA	25	25	9	16	0	0	0	0	16	284.0

[a] Nests that were already terminated when found, nests terminated by observers on the first visit, and nests of unknown fate were excluded from analyses.
[b] Total hatched differs from previous paper (Ohlendorf et al. 1986b) because criteria for inclusion differed (see Methods).

DUCKS

Few duck nests were found each year, so data from all 3 years were combined (by species) for analyses. Nest success of Gadwalls was significantly higher at Kesterson than at Volta (Table 3). A significantly larger proportion of Gadwall nests were deserted at Kesterson than at Volta, but this did not make up for the much higher predation rate at Volta (Table 4). No other between-location differences in nest success or cause-specific nest failure of ducks were detected, probably due to high variances associated with small sample sizes (particularly at Volta).

Dead or deformed embryos were found in successful nests of all three duck species at Kesterson but were rare at Volta (one dead and no deformed embryos in 3 years) (Table 5). Mean hatchability of duck eggs was lower at Kesterson, ranging from 71–90% (Table 5). However, there were too few successful nests at Volta to permit statistical comparisons of hatchability between the two sites.

AMERICAN COOTS

Like grebes, coots nested at Kesterson only in 1983. We found coot nests at Volta only in 1984 (Table 2), although brood observations indicated

TABLE 3. Estimates of percent nesting success (and 95% CI) of aquatic birds at Kesterson Reservoir and Volta Wildlife Area, 1983–1985.

Species and year(s)	Kesterson[a]	Volta[a]
Eared Grebe		
1983	72.6 (65.6–80.2)	—[b]
Mallard		
1983–1985	24.3 (12.1–48.3)	15.8 (2.5–92.2)
Cinnamon Teal		
1983–1985	7.1 (1.2–38.4)	20.1 (3.1–100)
Gadwall		
1983–1985[c]	22.9 (11.5–44.9)	1.7 (0.1–38.4)
American Coot		
1983	57.9 (45.6–73.5)	—[b]
1984	—[b]	5.7 (0.3–81.2)
Killdeer		
1984–1985	17.0 (8.0–35.3)	3.4 (0.2–57.3)
Black-necked Stilt		
1983	73.9 A (64.2–84.9)	46.3 A (21.5–97.4)
1984	7.5 C (4.8–11.6)	11.6 A (4.9–26.6)
1985[c]	34.6 B (24.3–49.1)	11.4 A (5.4–23.7)
American Avocet		
1983	87.2 A (66.6–100)	67.5 A (39.0–100)
1984	16.1 B (8.5–30.1)	18.9 B (10.8–32.9)
1985	31.4 B (17.4–56.1)	22.1 B (10.5–45.9)

[a] Within species and location, success estimates between years not sharing the same letters are significantly different (z-test, $P < 0.05$).
[b] No data.
[c] Kesterson and Volta success estimates are significantly different (z-test, $P < 0.05$).

that they also nested there in 1983 and 1985. Nearly 60% of the coot nests at Kesterson were successful (Table 3), with water-level changes and predation accounting for most nest failures (Table 4). Although embryotoxicosis was the cause of failure of only 6.3% of the nests (Table 4), it was responsible for failure of 29% of the eggs in successful nests (Table 5). Overall, embryotoxicosis was responsible for the failure of 34% of the eggs that survived to predicted hatching dates.

KILLDEER

Killdeer were only studied during 1984–1985. Data from these years were combined because so few nests were found at Volta (Table 2). Nest success at Kesterson was higher than at Volta, but confidence intervals were wide, and the difference was not statistically significant (Table 3). A significantly larger proportion of nests failed due to predation at Volta than at Kesterson (Table 4). Although no Killdeer nests failed due to embryotoxicosis, 4% of the eggs in successful nests at Kesterson failed due to embryotoxicosis, indicating that some females were adversely affected by selenium contamination despite the high rate of hatchability in the population (Table 5).

BLACK-NECKED STILTS

In 1985, nest success of stilts was significantly higher at Kesterson than at Volta (Table 3), due to the significantly higher predation rate at Volta (Table 4). There were no between-location differences in nest success of stilts in 1983 or 1984. Although predation rates differed significantly between locations those years, nest failures due to causes other than predation (e.g., changes in water level at Volta in 1984) offset the effects of predation.

At Kesterson, nest success of stilts was significantly different each year: it was highest in 1983 (73.9%), lowest in 1984 (7.5%), and intermediate in 1985 (34.6%) (Table 3). These differences were directly related to significantly different predation rates—lowest in 1983 (5.8%), highest in 1984 (86.9%), and intermediate in 1985 (56.0%) (Table 4). At Volta, nest success in stilts was highest in 1983, but due to the small sample size, confidence intervals were wide, and no significant between-year differences were detected.

Each year, embryotoxicosis was responsible for complete failure of a small percentage of stilt nests at Kesterson (Table 4), but many deformed embryos were found each year (Table 5). Embryotoxicosis was not observed in stilt nests at Volta. Of the effects (year, location, and year × location interaction) considered in the ANOVA of hatchability, only location was significant (F-test, $P = 0.009$). Thus, hatchability was significantly lower at Kesterson than at Volta, and between-year differences were not significant.

AMERICAN AVOCETS

We found no statistically significant between-location differences in nest success of avocets (Ta-

TABLE 4. Cause-specific failure rates (percentages and 95% CI) of nests of aquatic birds at Kesterson Reservoir (KR) and Volta Wildlife Area (VWA), 1983–1985.[a]

Species and year(s)	Predation		Desertion		Water level		Embryotoxicosis		Unknown	
	KR	VWA	KR	VWA	KR	VWA	KR	VWA	KR	VWA
Eared Grebe										
1983	4.2 (0.9–7.5)	—[b]	0	—[b]	5.6 (1.8–9.4)	—[b]	16.2 (10.1–22.2)	—[b]	1.4 (0–3.3)	—[b]
Mallard										
1983–1985	66.2 (47.1–85.4)	84.2 (55.6–100)	4.7 (0–13.8)	0	0	0	4.7 (0–13.8)	0	0	0
Cinnamon Teal										
1983–1985	82.5 (60.6–100)	53.3 (4.2–100)	0	26.6 (0–71.0)	0	0	0	0	10.3 (0–29.4)	0
Gadwall										
1983–1985	55.7 (36.2–75.2)	98.3* (92.8–100)	17.0* (1.9–32.0)	0	0	0	4.2 (0–12.4)	0	0	0
American Coot										
1983	14.7 (4.7–24.8)	—[b]	2.1 (0–6.2)	—[b]	16.8 (6.2–27.4)	—[b]	6.3 (0–13.2)	—[b]	2.1 (0–6.2)	—[b]
1984	—[b]	94.3 (78.4–100)	—[b]	0	—[b]	0	—[b]	0	—[b]	0
Killdeer										
1984–1985	79.2 (65.2–93.3)	96.6* (86.5–100)	0	0	0	0	0	0	3.8 (0–11.0)	0
Black-necked Stilt										
1983	5.8 C (0.3–11.3)	53.7* AB (18.7–88.6)	0 B	0 A	11.6* A (4.1–19.2)	0 B	2.9 A (0–6.9)	0 A	5.8* A (0.3–11.3)	0 A
1984	86.9* A (82.0–91.8)	46.0 B (27.9–64.0)	2.8* A (0.1–5.6)	0 A	0 B	42.4* A (24.5–60.4)	1.4 A (0–3.4)	0 A	1.4 A (0–3.4)	0 A
1985	56.0 B (43.1–68.9)	85.9* A (76.2–95.6)	7.5* A (0.4–14.5)	0 A	0 B	2.7 B (0–7.9)	1.9 A (0–5.5)	0 A	0 B	0 A
American Avocet										
1983	0 B	32.5 B (0–69.2)	0 A	0 A	12.8 A (0–36.2)	0 B	0 A	0 A	0 A	0 A
1984	78.6* A (66.7–90.5)	52.4 B (37.7–67.2)	5.2 A (0–12.3)	2.4 A (0–7.0)	0 A	23.8* A (11.0–36.6)	0 A	0 A	0 A	2.4 A (0–7.0)
1985	64.0 A (44.8–83.2)	77.9 A (61.5–94.2)	4.6 A (0–13.3)	0 A	0 A	0 B	0 A	0 A	0 A	0 A

[a] See Table 2 for number of nests included in analyses. Within species and location, cause-specific failure rates between years not sharing the same letters are significantly different (z-test, $P < 0.05$). Within species and years, asterisks denote significant between-site differences in cause-specific failure rates (z-test, $P < 0.05$).
[b] No data.

TABLE 5.   Hatchability of eggs in successful nests at Kesterson Reservoir (KR) and Volta Wildlife Area (VWA).

| Species and year(s) | Site | Sample sizes | | No. eggs hatched | No. egg failures due to embryotoxicosis | | | | Hatchability $\bar{x} \pm$ SE |
		Nests[a]	Eggs		De-formed	Dead	Unde-veloped	Un-known[b]	
Eared Grebe									
1983	KR	109	324	220	11	62	18	13	69.8 ± 2.69
Mallard									
1983–1985	KR	21	173	155	1	5	11	1	87.3 ± 4.37
1983–1985	VWA	3	17	16	0	1	0	0	95.2 ± 4.76
Cinnamon Teal									
1983–1985	KR	5	42	38	0	4	0	0	90.0 ± 10.0
1983–1985	VWA	2	18	18	0	0	0	0	100
Gadwall									
1983–1985	KR	12	98	69	9	10	4	6	71.4 ± 8.11
American Coot									
1983	KR	40	303	214	20	36	27	6	71.1 ± 3.79
Killdeer									
1984–1985	KR	17	51	49	1	1	0	0	96.1 ± 3.92
1984–1985	VWA	1	2	2	0	0	0	0	100
Black-necked Stilt									
1983	KR	92	337	306	17	6	7	1	90.9 ± 1.91
1983	VWA	7	28	28	0	0	0	0	100
1984	KR	48	150	144	3	2	0	1	95.5 ± 2.03
1984	VWA	5	15	15	0	0	0	0	100
1985	KR	47	137	119	14	2	2	0	87.6 ± 2.88
1985	VWA	10	32	32	0	0	0	0	100
American Avocet									
1983	KR	16	55	54	0	0	1	0	98.4 ± 1.56
1983	VWA	8	31	31	0	0	0	0	100
1984	KR	17	52	52	0	0	0	0	100
1984	VWA	24	73	70	0	2	1	0	96.2 ± 2.13
1985	KR	19	51	46	4	1	0	0	91.2 ± 3.46
1985	VWA	9	23	23	0	0	0	0	100

[a] Some nests with eggs with unknown fates were deleted from hatchability analyses (see Methods).
[b] Eggs that failed to hatch but were unexamined.

ble 3). Predation was significantly higher at Kesterson than Volta in 1984, but this difference was offset by flooding-induced nest losses at Volta (Table 4).

Nest success was significantly higher at both locations in 1983 than in 1984 or 1985 (Table 3). At Kesterson these differences were related mainly to significantly lower predation in 1983 (Table 4). Predation on avocet nests was significantly higher at Volta in 1985 than in 1983, and was responsible for significant differences in nesting success between those years (Tables 3 and 4). The combination of predation and flooding destroyed 76% of the nests at Volta in 1984, and resulted in significantly lower nesting success in 1984 relative to 1983 (Tables 3 and 4).

No avocet nests failed due to embryotoxicosis at either location (Table 4), and hatchability was greater than 90% at both locations in all years (Table 5). Deformities were observed only at Kesterson in 1985. In the ANOVA of hatchability only the interaction term was significant (F-test, $P = 0.03$). At Kesterson, hatchability was significantly lower in 1985 than in 1984 (Bonferroni mean separation test, $P < 0.05$). No other between-year or between-location differences in hatchability were significant.

DISCUSSION

Assessment of impacts of environmental contaminants on wild birds often involves field studies where physiological or life history characteristics of birds from contaminated areas are

statistically compared to data from concurrently studied uncontaminated areas (Hill and Fleming 1982, Henny 1987). When reproductive success is the life history characteristic of concern, Mayfield method estimates of nest success are appropriate. These methods produce estimates suitable for statistical comparisons, and despite potential problems, are less biased than traditional methods (Mayfield 1975).

Potential problems with the Mayfield method are: (1) underestimation of nest success per nesting female when birds renest, (2) large variances when sample sizes are small, (3) potentially biased estimates when daily survival rates are not constant throughout the study, (4) inability to provide estimates of cause-specific nest failure, and (5) inability to assess the importance of partial nest failure.

Because birds in our study were not individually marked, assessment of the rate of renesting was impossible, and nest success and failure rates are on a per nesting attempt rather than per nesting female basis (Erwin and Custer 1982). Most species that we studied are known to renest (Gullion 1954, Gates 1962, Hunt and Anderson 1966, Gibson 1971, Pospahala et al. 1974, Nol and Lambert 1984), thus our success estimates potentially underestimate nesting success per female.

Sample sizes of at least 20 nests are recommended for Mayfield method estimates (Hensler and Nichols 1981). We could not always find 20 nests of each species per year and location. With small sample sizes, especially at Volta, variances were frequently large and confidence intervals wide; thus relatively large differences in nesting success were not always statistically significant (e.g., between-location differences in nesting success of stilts in 1983).

The constancy of daily nest-survival rates throughout the interval of study can be tested, but large sample sizes are required (Klett and Johnson 1982). However, the Mayfield method is robust to violations of this assumption, and mild variability in daily survival rates should not affect the validity of nest success estimates (Klett and Johnson 1982).

In addition to providing a Mayfield-method estimate of nest success, MICROMORT enabled us to assess cause-specific nest failure (Heisey and Fuller 1985). This technique has also been used to estimate rates of snake predation on turtle-dove nests (Conry 1988), and is an important methodological advance in the study of nesting birds.

Mayfield method and cause-specific nest failure estimates usually assess success and failure at the level of nests rather than eggs; thus a nest is considered successful even if the majority of the clutch fails to hatch. Aquatic birds affected by selenium contamination often experienced partial clutch failure in this study, but we were able to address the problem of partial losses by using hatchability estimates. Such estimates are useful for evaluating the effects of contaminants on reproduction of avian populations (Ohlendorf et al. 1985, DeSmet 1987).

We recommend cause-specific nest failure and hatchability estimates as complementary methods of assessing contaminant-related impairment of reproduction in avian populations. Investigators using these techniques should strive for large sample sizes in affected and control areas, and, if practical, attempt to assess the rate of renesting by studying marked individuals.

ACKNOWLEDGMENTS

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