THE INFLUENCE OF PARTIAL CLUTCH DEPREDATION ON DUCKLING PRODUCTION

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Abstract: Nest depredation is the foremost cause of reproductive failure in waterfowl. Management strategies typically have focused on reducing predator contact with nests, yet the fate of nests after predators have found them has received little attention. Although nest depredation can result in complete clutch loss, nests often are only partially depredated and the remaining clutch may be successful. We investigated the prevalence of partial clutch depredation in dabbling ducks and assessed its influence on duckling production in the Suisun Marsh of California, USA, from 1998 to 2000. Partial clutch depredation by predators was common in all duck species and in all years. Overall, 37% of mallard (*Anas platyrhynchos*; $n = 803$), 37% of gadwall (*A. strepera*; $n = 340$), 22% of northern pintail (*A. acuta*; $n = 46$), 31% of cinnamon teal (*A. cyanoptera*; $n = 16$), and 1 of 2 northern shoveler nests (*A. clypeata*) were partially depredated. Of those nests experiencing a depredation event, 53% of mallard and 50% of gadwall nests were only partially depredated rather than completely destroyed. As a result of partial clutch depredation, total duckling production was reduced by 10% for mallards and 9% for gadwalls. The female's decision to stay with or abandon the reduced clutch had an important influence on nest success. Mallard and gadwall females abandoned the nesting attempt after partial clutch depredation 37% and 32% of the time, respectively. However, 27% of partially depredated mallard nests and 23% of partially depredated gadwall nests were successful. Egg success was 0.60 ± 0.24 (mean $\pm$ SD) for mallards and 0.53 ± 0.23 for gadwall. From 1998 to 2000, 22% of mallard and 21% of gadwall ducklings produced in our study area came from partially depredated nests. Although many duck nests experienced partial clutch loss, they nevertheless contributed substantially to overall duckling production. Incorporating an estimate of egg success, in addition to nest success, may provide a more accurate assessment of waterfowl management strategies.

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Predators are the primary cause of duck nest failure and can significantly limit recruitment (Sargeant and Raveling 1992), potentially below replacement levels for mallards (Cowardin et al. 1985) and other species (Greenwood et al. 1995, Klett et al. 1988). As a result, waterfowl management strategies have focused on reducing predator contact with nests through predator exclosures or removal (Lokemoen and Woodward 1993, Sargeant et al. 1995, Garrettson and Rohwer 2001) and planting dense nesting cover (reviews by Cowardin et al. 1985, Clark and Nudds 1991, McKinnon and Duncan 1999). Researchers also have investigated the effects of predator composition and abundance (Johnson et al. 1989, Sovada et al. 1995), supplemental prey (Crabtree and Wolfe 1988, Greenwood et al. 1998), and alternate prey (Byers 1974, Ackerman 2002*a*) on nest-depredation rates. However, researchers and managers rarely have considered the actual fate of nests after predators have found them. Although nest depredation can result in complete clutch loss, in many cases nests are only partially depredated (e.g., Choate 1967, Grand and Flint 1997, Larivière and Messier 1997), and the remaining clutch may still be successful. Partial clutch loss occurs when predators either are unable or disinclined (e.g., satiation) to consume an entire clutch and therefore leave some eggs intact.

Partial clutch depredation potentially influences duckling production in 3 ways. First, it may reduce the probability of a nest being successful, either because the female abandons the remaining eggs (Armstrong and Robertson 1988, Ackerman et al. 2003) or the nest becomes more susceptible to further depredation events (Choate 1967, Larivière and Messier 1997). Second, if the female stays with the reduced clutch, fewer eggs remain in the nest with the potential to hatch. Third, if the female stays with the nest and the nest is successful, the remaining eggs in the

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reduced clutch may have reduced hatching success. For example, prolactin levels in captive female mallards decreased after partial clutch loss, which caused the brood patch to deteriorate and resulted in reduced hatching success of the remaining eggs (Hall 1987). Thus, partial clutch depredation has important implications for duckling production.

Management strategies designed to increase waterfowl production typically are assessed using the Mayfield estimate of nest success (e.g., Sargeant et al. 1995, Greenwood et al. 1998, McKinnon and Duncan 1999, Garrettson and Rohwer 2001); however, this measure does not fully incorporate the effects of partial clutch depredation. For example, although a partially depredated nest that hatches ≥1 egg is considered successful when calculating Mayfield nest success (Klett et al. 1986), the number of eggs hatching within a successful nest often is not reported. In areas with high rates of partial clutch depredation, the number of eggs hatching in a successful nest can be significantly reduced. Therefore, duckling production would be better estimated if both nest success and egg success were reported.

On the other hand, estimates of waterfowl production that incorporate measures of both nest success and egg success inherently take partial depredation events into account. Yet, the proportion of duckling production lost to partial clutch depredation and the amount of production contributed by partially depredated nests typically is unknown. Management strategies would benefit from this knowledge because predators and predator behaviors that partially depredate clutches may be different than those that completely destroy the clutch (Johnson et al. 1992, Larivière and Messier 1997). Understanding which predators and behaviors are most detrimental to duckling production depends on knowing not only the number of nests depredated, but also the magnitude of clutch loss. Predators and behaviors that result in a clutch being partially consumed may not influence duckling production to the same extent as predators and behaviors that completely destroy a nest. Thus, management strategies may vary depending on the extent to which duckling production is reduced by partial rather than complete clutch depredation.

Our objectives were to (1) quantify the prevalence of partial clutch depredation, (2) assess its influence on both nest success and egg success, and (3) determine both the amount of duckling production lost to partial clutch depredation and the amount of production contributed by partially depredated nests. We reported high rates of partial clutch depredation in 5 species of upland nesting dabbling ducks and used mallard and gadwall nests to examine the extent, magnitude, and fate of partially depredated clutches over a 3-year period during which annual nest success varied.

STUDY AREA

The Grizzly Island Wildlife Area is located in the center of Suisun Marsh, a large (approx 34,000 ha) brackish estuary at the downstream end of the Sacramento–San Joaquin Delta in California, USA (38°08′N, 121°59′W). The Grizzly Island Wildlife Area contains roughly 2,000 ha of wetlands and 1,600 ha of uplands managed for waterfowl production. We conducted nest searches within upland fields during the 1998, 1999, and 2000 duck nesting seasons, searching 222, 219, and 230 ha each year, respectively. We examined a broad range of representative habitats within our study area, although fields searched for nesting ducks were not randomly selected due to logistical constraints. These uplands are managed by the California Department of Fish and Game on a per-field basis for different vegetation types and structure, including fields dominated by pickleweed (*Salicornia virginica*), vetch (*Vicia* spp.), herbs (*Atriplex patula, Lotus corniculatus*), mid-height (<1 m) grasses (*Lolium* spp., *Hordeum* spp., *Bromus* spp., *Polypogon monspeliensis*), or taller (>1 m) grasses (*Elytrigia* spp., *Phalaris* spp.).

METHODS

Nest Searching and Monitoring Techniques

Waterfowl nest search procedures were designed following Klett et al. (1986) as modified by McLandress et al. (1996) for our study site. Nest searches began in early April and continued until July to ensure that both early- and late-nesting ducks would be found (McLandress et al. 1996). Each field was searched at 3-week intervals 4–5 times until no new nests were found. Nest searches typically began at least 2 hr after sunrise and were finished by 1400 hr to avoid missing nests while females were on morning and afternoon nest breaks (Caldwell and Cornwell 1975, Gloutney et al. 1993).

We conducted nest searches using a 50-m nylon rope strung between 2 slow-moving all-terrain vehicles. Tin cans containing stones to generate noise were attached at 1.5-m intervals along the length of the rope. The rope was dragged through the vegetation, causing females to flush from their nests, thus enabling observers to find those nests by searching a restricted area. Each nest was marked with a 2-m bamboo stake placed 4 m north of the nest bowl and a shorter stake placed just south of the nest bowl, level with the vegetation height. We revisited each nest on foot once every 7 days, determined the stage of embryo development by candling (Weller 1956), and recorded clutch size and nest fate (hatched, destroyed, or abandoned).

We considered a nest successful if at least 1 egg hatched (as determined from shell remains; Klett et al. 1986). After each visit, we covered the eggs with nest material, as the female would have done before leaving for an incubation recess. Nests that were abandoned on the day we found them, or were partially depredated before we found them, were excluded from all analyses (Klett et al. 1986). We also excluded nests that were disturbed by investigators, such as nests that were altered by clutch-size manipulations (Ackerman 2002*b*) and those damaged by nest searching or egg handling procedures (Klett et al. 1986).

We calculated nest success using Mayfield (1961, 1975) techniques modified for waterfowl (Johnson 1979). Nest-initiation date was calculated by subtracting the age of the nest when found (i.e., the number of eggs when found plus the incubation stage when found) from the date the nest was discovered (Klett et al. 1986).

Partial Clutch Depredation

We considered a nest partially depredated when the clutch size was reduced between consecutive investigator visits and at least 1 egg was still intact in the nest bowl. For laying-stage nests (when clutch sizes increase between consecutive investigator visits), we assumed that females laid 1 egg per day and began incubating the eggs upon the termination of laying (Afton and Paulus 1992). Therefore, we suspected a laying-stage nest had been partially depredated when the number of eggs in the nest was smaller than expected based on laying rates. We confirmed that a partial depredation event had occurred in these nests by using eggshell evidence remaining near the nest-site; otherwise, we excluded the nest from further analyses.

We categorized partially depredated nests as having either eggs missing or eggshell fragments present within 3 m of the nest. The date of partial depredation was estimated as the midpoint between discovery of the depredation event and the preceding visit (maximum error of ±3.5 days), and the incubation stage at the time of the partial depredation event was defined as the number of days the eggs had been incubated prior to that date. If the partial depredation event caused the female to abandon the nest, then we also used the arrested development of the embryo in the remaining eggs to determine the stage of incubation at which the depredation event occurred (via candling; Weller 1956). We continued to monitor partially depredated nests until their fate (hatched, destroyed, or abandoned) was determined. When multiple partial clutch depredations occurred, we based our analyses on the first partial clutch loss unless otherwise indicated.

Nest Desertion

Nest desertion from partial clutch loss was determined from multiple clues, including female absence, egg temperature, down placement, and arrested embryonic development (Klett et al. 1986). A nest was considered to be active (non-abandoned) if we flushed the female from the nest subsequent to the partial depredation event (abandonment generally occurs within 24 hr of clutch loss; Armstrong and Robertson 1988). If we were uncertain of a nest's status (i.e., abandoned or non-abandoned), we revisited the nest within 7 days to confirm that the female had either abandoned or stayed with the reduced clutch. If we still were uncertain of the nest's status following the partial depredation event (e.g., if we found the nest further depredated upon our revisit), we excluded the nest from analyses of nest desertion. Additionally, nests with evidence that the female had been killed during the partial depredation event were excluded from analyses of nest desertion.

Egg Success

Egg success, also known as hatching success, was defined as the number of ducklings hatching in a successful nest divided by the total clutch size (Sargeant and Raveling 1992). Egg success of partially depredated nests was calculated for (1) the initial clutch size, and (2) the remaining eggs after the final partial depredation event. The first was calculated by dividing the number of eggs that hatched by the initial clutch size before a partial depredation event occurred. The second was calculated by dividing the number of eggs that hatched by the clutch size remaining after the final partial depredation event (hereafter referred to as the remaining clutch size). Egg success of intact nests was calculated by dividing the number of eggs that hatched by the complete clutch size. Only nests considered to have a "complete clutch" were used in determining the egg success of intact clutches. Complete clutch size was defined as the total number of eggs laid before the incubation period began (Afton and Paulus 1992). Nests with eggs incubated >8 days upon discovery were excluded from complete clutch status (and not used in analyses) due to high rates of partial clutch depredation and the resultant uncertainty that nests still contained all eggs that were originally laid. Only successful nests (≥1 egg hatched) were used to calculate egg success. Additionally, we included only nests in which we could determine with confidence the number of eggs that hatched (as determined from shell remains; Klett et al. 1986).

Duckling Production

We estimated production using the formula: [no. of ducklings = [no. of successful nests] × [mean clutch size] × [mean egg success]]. We used this formula to estimate the number of ducklings produced from the area we searched during our study. We calculated both the total duckling production and the production from partially depredated nests only. Additionally, we estimated the number of ducklings lost to partial clutch depredation using the formula: (no. of ducklings lost to partial clutch depredation = [no. of partially depredated nests that were successful] × [mean clutch size] × [(mean egg success of intact nests) − (mean egg success of partially depredated nests)]]. Using these formulas, we estimated the proportion of ducklings produced from partially depredated nests and the proportion lost to partial clutch depredation.

Statistical Analyses

We used Mann-Whitney *U* tests, corrected for ties, to compare the number of eggs depredated in each eggshell category (i.e., partially depredated nests with eggs missing or eggshells evident within 3 m of the nest), and to compare egg success among partially depredated and intact nests. We used *t*-tests to compare clutch sizes among nests that either were partially depredated or completely destroyed when first found. Logistic regression was used to analyze the likelihood of a nest being partially depredated rather than being completely destroyed (when the nest was first found) throughout the nesting season. We conducted analyses on pooled data for all years unless otherwise specified. All means are reported ±1 SD.

RESULTS

We found 1,222 (803 usable for partial clutch depredation analysis) mallard, 401 (340) gadwall, 48 (46) northern pintail, 18 (16) cinnamon teal, and 2 (2) northern shoveler nests in 671 ha during the 1998–2000 waterfowl nesting seasons. Overall, mallard nest success ranged from 8.7% (95% CI: 6.3 to 11.9%) in 1998 and 8.2% (5.6 to 11.9%) in 1999 to 33.6% (28.5 to 39.6%) in 2000. Gadwall nest success was 12.0% (95% CI: 8.2 to 17.4%) in 1998, 2.6% (1.0 to 6.9%) in 1999, and 26.0% (18.5 to 36.5%) in 2000. This yearly variation in nest success allowed us to assess the influence of partial clutch depredation during different intensities of nest depredation common to our study site (McLandress et al. 1996). Due to small sample sizes of northern pintail, cinnamon teal, and northern shoveler nests, we used mallard and gadwall nests for most analyses of partial clutch depredation.

Partial Clutch Depredation

Partial clutch loss by predators was common in all duck species and in all years. Overall, 37% of mallard nests were partially depredated, ranging from 27% in 1999 to 42% in 1998 (Table 1). Similarly, 37% of gadwall, 22% of northern pintail, 31% of cinnamon teal, and 1 of 2 northern shoveler nests were partially depredated. Of those nests experiencing a depredation event, 53% of mallard and 50% of gadwall nests were partially depredated, rather than completely destroyed, when first found by a predator (Table 1).

Partial clutch depredation was common throughout the nesting season (Fig. 1). Julian nest-initiation date did not influence the likelihood of being partially depredated for mallard nests (n = 803; likelihood ratio $\chi^2 = 0.66$, $r^2 < 0.01$, $P = 0.42$), whereas gadwall nests tended to be partially depredated more often earlier in the nesting season (n = 340; likelihood ratio $\chi^2 = 9.05$, $r^2 = 0.02$, $P = 0.003$). Gadwall nest-initiation dates averaged 16 days later than those of mallards.

Partial clutch depredation was common throughout incubation and resulted in a wide range of remaining clutch sizes (Figs. 2, 3). Initial clutch sizes were 8.6 ± 1.5 eggs for mallards and 9.5 ± 1.7 eggs for gadwalls during 1998–2000. The initial clutch size did not affect the outcome of a predator depredating a nest (i.e., either partially

Table 1. Frequency of occurrence, number of eggs lost, and fate of partially depredated mallard and gadwall nests from 1998 to 2000 in the Suisun Marsh, California, USA.

	Mallard				Gadwall			
	1998	1999	2000	Total	1998	1999	2000	Total
Total nests[a]	238	167	398	803	177	54	109	340
Depredated nests[b]								
n	202	137	225	564	134	46	75	255
Frequency	85%	82%	57%	70%	76%	85%	69%	75%
Partially depredated (PD)[c]								
n	100	45	156	301	64	13	50	127
Frequency PD of total nests	42%	27%	39%	37%	36%	24%	46%	37%
Frequency PD of depredated nests	50%	33%	69%	53%	48%	28%	67%	50%
Fate of partially depredated nests[d]								
Abandoned [e]								
Minimum estimate								
n	53/100	21/45	37/156	111/301	26/64	5/13	10/50	41/127
Frequency	53%	47%	24%	37%	41%	38%	20%	32%
Maximum estimate								
n	53/90	21/38	37/145	111/273	26/58	5/9	10/48	41/115
Frequency	59%	55%	26%	41%	45%	56%	21%	36%
Hatched								
n	11	4	66	81	15	0	14	29
Frequency	11%	9%	42%	27%	23%	0%	28%	23%
Frequency hatched when hens stay[f]								
Minimum estimate	23%	17%	55%	43%	39%	0%	35%	34%
Maximum estimate	30%	24%	61%	50%	47%	0%	37%	39%
Other unsuccessful[g]								
n	36	20	53	109	23	8	26	57
Frequency	36%	44%	34%	36%	36%	62%	52%	45%
Eggs lost from partial depredation[d]								
Mode	1	1	1	1	1	1	1	1
Mean ± SD	3.18 ± 2.13	3.31 ± 2.34	2.89 ± 2.01	3.05 ± 2.10	3.25 ± 2.30	3.54 ± 2.37	3.10 ± 2.31	3.22 ± 2.30
Proportion of clutch lost ± SD	0.41 ± 0.25	0.37 ± 0.24	0.35 ± 0.23	0.37 ± 0.24	0.36 ± 0.24	0.40 ± 0.26	0.33 ± 0.23	0.35 ± 0.24

[a] Excludes nests that were research abandoned, investigator manipulated or disturbed, and nests already partially depredated when found (Klett et al. 1986). All analyses are based on these nests.
[b] Includes nests that experienced any type of partial or complete depredation.
[c] Includes nests that were partially depredated either once or multiple times.
[d] All analyses were done on the first partial depredation event.
[e] We calculated both a minimum and maximum frequency of abandonment. The minimum estimate includes all partially depredated nests. The maximum estimate excludes partially depredated nests that we were unable to determine the hen's decision to stay or abandon and the nest was depredated again before we could recheck the nest (see Methods).
[f] We calculated both a minimum and maximum frequency of nests hatching when hens stayed with partially depredated nests. Sample size was similar to subscript e.
[g] Includes all nests that were terminated after the first partial depredation, including subsequent nest depredation events and nest abandonment.

depredated or completely destroyed; mallard: $t = 0.17$, df = 396, $P = 0.87$; gadwall: $t = 0.20$, df = 184, $P = 0.85$). Mallard nests lost an average of 3.05 ± 2.10 eggs or 37 ± 24% of the clutch during the first partial depredation event. Similarly, gadwall nests lost 3.22 ± 2.30 eggs, or 35 ± 24% of the clutch. Most commonly, partial clutch depredation resulted in the loss of only 1 egg, regardless of nesting species or year (Table 1).

Partially depredated nests frequently had eggs missing without other evidence such as eggshells or yolk that would indicate that a predator had disturbed the clutch (Table 2). Fewer eggs were lost from mallard nests with eggs missing (2.15 ± 1.52 eggs or 26 ± 18% of the clutch) than from nests with eggshells evident (3.82 ± 2.22 eggs or 47 ± 25% of the clutch; $Z = 6.96$, $P < 0.0001$). Similarly, gadwalls lost fewer eggs from nests with evidence of eggs missing (2.33 ± 1.66 eggs or 25 ± 17% of the clutch) than from nests with eggshells evident (4.60 ± 2.47 eggs or 50 ± 25% of the clutch; $Z = 5.32$, $P < 0.0001$; Table 2).

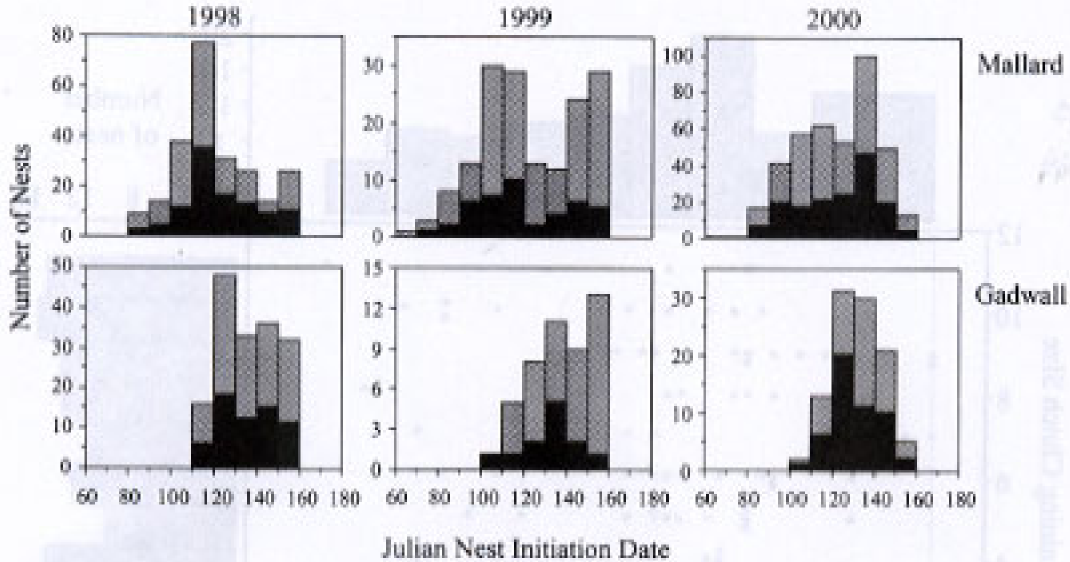

Fig. 1. The number of mallard and gadwall nests that were partially depredated (filled) out of the total number of nests (shaded) initiated by date during the 1998–2000 nesting seasons in the Suisun Marsh, California, USA.

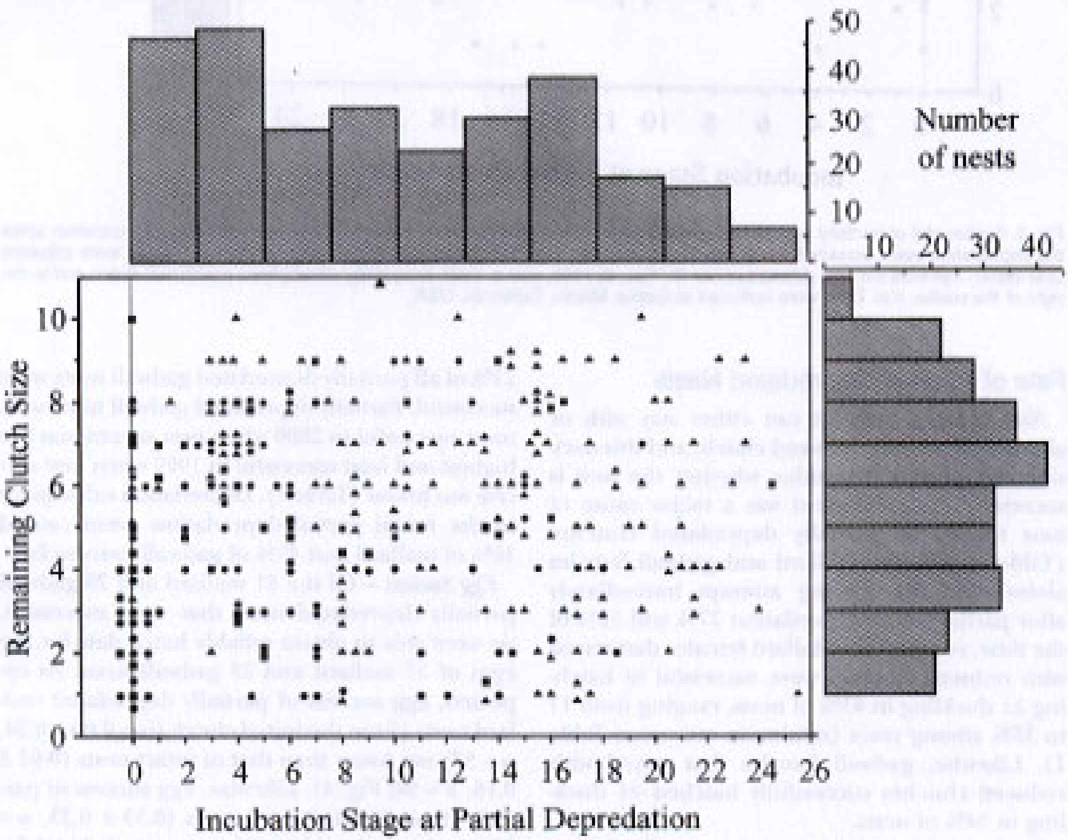

Fig. 2. Scatter plot of partially depredated mallard nests with respect to the remaining clutch size and stage of incubation when the depredation event occurred. Each data point indicates a partial depredation event; overlapping data points were adjusted until visible. Symbols indicate different years: ● 1998, ■ 1999, and ▲ 2000. Frequency distributions are shown above and to the right of the scatter plot. Data were collected at Suisun Marsh, California, USA.

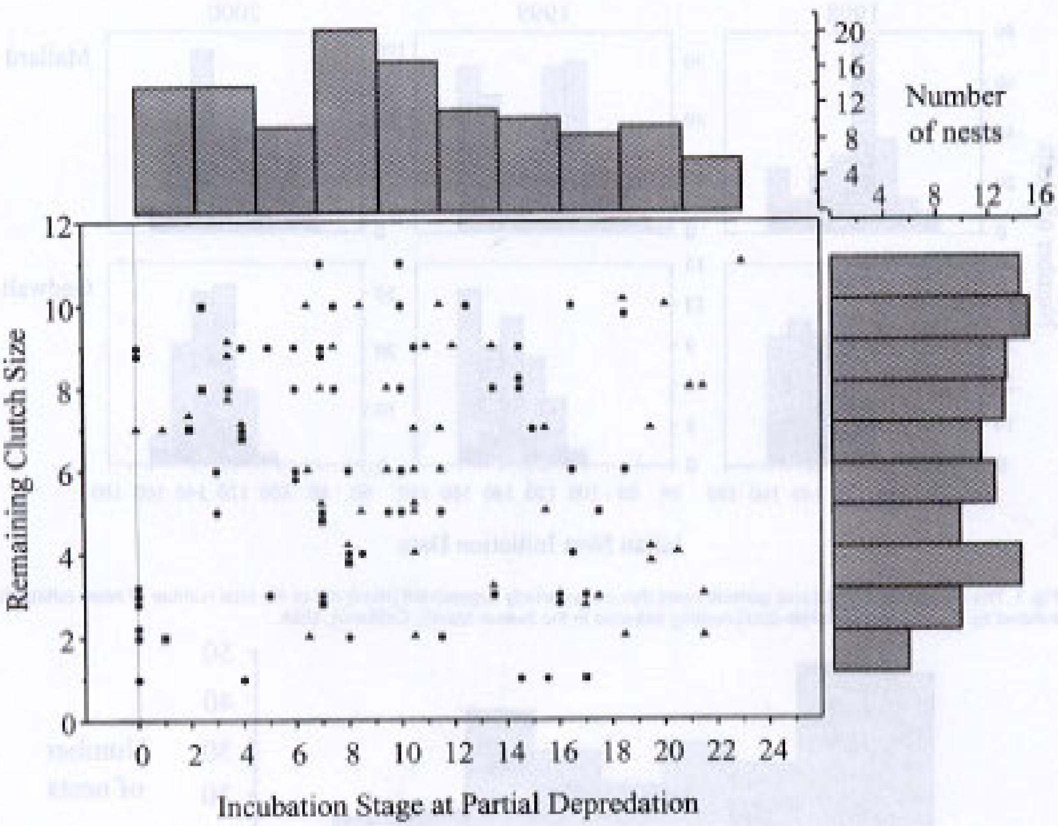

Fig. 3. Scatter plot of partially depredated gadwall nests with respect to the remaining clutch size and stage of incubation when the depredation event occurred. Each data point indicates a partial depredation event; overlapping data points were adjusted until visible. Symbols indicate different years: ● 1998, ■ 1999, and ▲ 2000. Frequency distributions are shown above and to the right of the scatter plot. Data were collected at Suisun Marsh, California, USA.

Fate of Partially Depredated Nests

Nest Success.—Females can either stay with or abandon a partially reduced clutch, and this decision will in part determine whether the nest is successful. Abandonment was a major cause of nest failure of partially depredated clutches (Table 1). Overall, mallard and gadwall females abandoned the nesting attempt immediately after partial clutch depredation 37% and 32% of the time, respectively. Mallard females that stayed with reduced clutches were successful in hatching ≥1 duckling in 43% of nests, ranging from 17 to 55% among years (minimum estimates; Table 1). Likewise, gadwall females that stayed with reduced clutches successfully hatched ≥1 duckling in 34% of nests.

Across years, partially depredated mallard nests were successful 27% of the time, ranging from 11% (1998) and 9% (1999) when nest success was low to 42% (2000) when nest success was high. Similarly, 23% of all partially depredated gadwall nests were successful. Partially depredated gadwall nests were most successful in 2000 when nest success was the highest and least successful in 1999 when nest success was lowest (Table 1). Depredation subsequent to the initial partial depredation event caused 36% of mallard and 45% of gadwall nests to fail.

Egg Success.—Of the 81 mallard and 29 gadwall partially depredated nests that were successful, we were able to obtain reliable hatch data for the eggs of 57 mallard and 25 gadwall nests. As expected, egg success of partially depredated mallard nests (from the initial clutch size; 0.60 ± 0.24, n = 57) was lower than that of intact nests (0.92 ± 0.16, n = 94; Fig. 4). Likewise, egg success of partially depredated gadwall nests (0.53 ± 0.23, n = 25) was lower than that of intact nests (0.79 ± 0.26, n = 36; Fig. 4). However, when we considered only the remaining eggs in partially depredated nests (e.g., Hall 1987), egg success was not significantly

Table 2. Number of mallard and gadwall eggs lost to partial clutch depredation during 1998–2000 in the Suisun Marsh, California, USA. Partially depredated nests were categorized according to the depredated eggs as either having egg(s) missing or egg shell(s) evident at the nest.

	No. of eggs depredated in nests with egg(s) missing				No. of eggs depredated in nests with egg shell(s) evident			
	1998	1999	2000	Total	1998	1999	2000	Total
Mallard								
Sample size (nests)	38	14	86	138	62	31	70	163
Mode	1	1	1	1	4	1	1	1
Mean ± SD	1.76 ± 1.26	2.21 ± 1.76	2.30 ± 1.67	2.15 ± 1.52	4.05 ± 2.09	3.81 ± 2.43	3.61 ± 2.24	3.82 ± 2.22
Proportion of clutch lost ± SD	0.23 ± 0.16	0.26 ± 0.20	0.27 ± 0.18	0.26 ± 0.18	0.52 ± 0.23	0.43 ± 0.24	0.44 ± 0.26	0.47 ± 0.25
Gadwall								
Sample size (nests)	41	8	28	77	23	5	22	50
Mode	1	1	1	1	5	7	2	5
Mean ± SD	2.29 ± 1.36	2.38 ± 1.60	2.36 ± 2.06	2.33 ± 1.66	4.96 ± 2.64	5.40 ± 2.30	4.05 ± 2.30	4.60 ± 2.47
Proportion of clutch lost ± SD	0.25 ± 0.15	0.27 ± 0.18	0.25 ± 0.19	0.25 ± 0.17	0.65 ± 0.26	0.62 ± 0.24	0.43 ± 0.24	0.50 ± 0.25

lower than that of intact mallard (0.85 ± 0.23, n = 57; $Z = 1.18$, $P = 0.24$) or gadwall nests (0.74 ± 0.27, n = 25; $Z = 0.73$, $P = 0.47$; Fig. 4).

Duckling Production

From 1998 to 2000, 274 mallard and 104 gadwall nests hatched, producing an estimated 1,907 mallard and 706 gadwall ducklings (Table 3). Of these, 29.6% of successful mallard and 27.9% of successful gadwall nests had been partially depredated. Therefore, 21.9% and 20.7% of the total number of mallard and gadwall ducklings produced came from partially depredated nests (Table 3). Although yearly sample sizes of successful nests are small, partially depredated mallard and gadwall nests consistently produced >20% of the total number of ducklings each year (Table 3), except for gadwalls in 1999 when we found few nests and none of the partially depredated nests (n = 13) hatched (Table 1).

We also determined the degree to which duckling production was reduced by partial depredation events in nests where females stayed with reduced clutches and were successful. Because these nests were partially depredated rather than remaining completely intact, total duckling production was reduced by 10.3% for mallards and 9.3% for gadwalls (Table 3).

DISCUSSION

Partial clutch depredation was common in all duck species in all years. We found that 37% of all duck nests were partially depredated. Further, of the nests that experienced a depredation event, 52% were partially depredated rather than totally destroyed when first found by a predator. In the

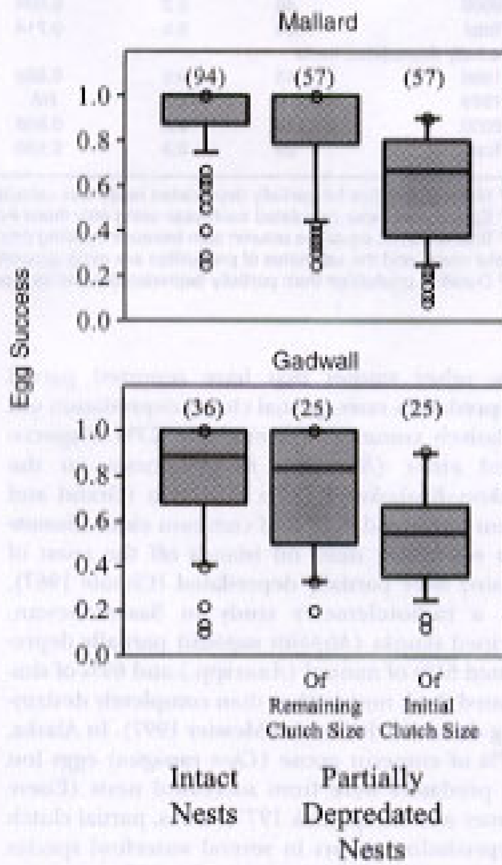

Fig. 4. Box plots of egg success for successful mallard and gadwall nests during 1998–2000 in the Suisun Marsh, California, USA. For both mallard and gadwall, egg success of nests partially depredated from the initial clutch size was lower than that of intact nests. However, we found no significant difference between egg success of the remaining eggs in partially depredated nests and intact nests. Sample sizes (number of nests) are indicated in parentheses.

Table 3. Mallard and gadwall duckling production from partially depredated nests during 1998–2000 in the Suisun Marsh, California, USA.

	Successful nests	Clutch size[a]	Egg success[b]	Duckling production: Number[c]	Duckling production: From partially depredated nests[d]	Duckling production: Lost to partial depredation
Mallard						
All nests						
1998	35	8.6	0.768	231	–	10.9%
1999	17	8.6	0.848	124	–	5.1%
2000	222	8.6	0.813	1,551	–	10.9%
Total	274	8.6	0.809	1,907	–	10.3%
Partially depredated nests						
1998	11	8.6	0.611	58	25.0%	–
1999	4	8.6	0.752	26	20.9%	–
2000	66	8.6	0.578	328	21.2%	–
Total	81	8.6	0.601	418	21.9%	–
Gadwall						
All nests						
1998	51	9.9	0.806	407	–	10.1%
1999	7	9.3	1.000	65	–	0%
2000	46	9.2	0.604	256	–	6.8%
Total	104	9.5	0.714	706	–	9.3%
Partially depredated nests						
1998	15	9.9	0.589	87	21.5%	–
1999	0	9.3	NA	0	0%	–
2000	14	9.2	0.506	65	25.6%	–
Total	29	9.5	0.530	146	20.7%	–

[a] Mean clutch size for partially depredated nests was calculated each year using all nests known to have a complete clutch.
[b] Egg success was calculated each year using only those nests known to have a complete clutch.
[c] Total does not equal the column sum because duckling production was estimated each year using small sample sizes of successful nests, and the estimates of production are more accurate when combining data from all years.
[d] Duckling production from partially depredated nests as a percent of the total production.

few other studies that have reported partial depredation rates, partial clutch depredation was relatively common. For example, 23% of spectacled eider (*Somateria fischeri*) nests on the Yukon–Kuskokwim Delta in Alaska (Grand and Flint 1997) and 9–13% of common eider (*Somateria mollissima*) nests on islands off the coast of Maine were partially depredated (Choate 1967). In a radiotelemetry study in Saskatchewan, striped skunks (*Mephitis mephitis*) partially depredated 61% of natural (*Anas* spp.) and 69% of simulated duck nests rather than completely destroying them (Larivière and Messier 1997). In Alaska, 57% of emperor goose (*Chen canagica*) eggs lost to predators were from successful nests (Eisenhauer and Kirkpatrick 1977). Thus, partial clutch depredation occurs in several waterfowl species and waterfowl production areas. However, no attempt has been made to quantify duckling production lost to this type of depredation event.

Although partial clutch depredations reduced duckling production by 9–10% in our study, partially reduced clutches nonetheless contributed substantially to duckling production (Table 3). The likelihood of success for partially depredated nests depends on a number of factors (Fig. 5).

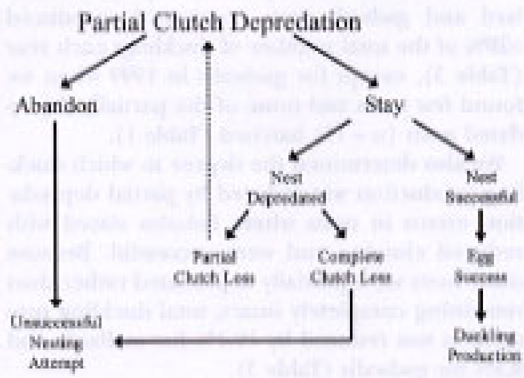

Fig. 5. A transition tree depicting the components of partial clutch depredation that influence duckling production. After partial clutch depredation, a female decides whether to stay with or abandon the reduced clutch. Nest desertion results in an unsuccessful nesting attempt. If the female stays, the nest either will be successful, with duckling production being influenced by egg success, or will be further depredated, either completely or partially. Complete clutch loss results in an unsuccessful nesting attempt, whereas partial clutch loss results in the female making another decision to stay or abandon.

When partial clutch loss occurs, the decision of the female to either stay with or abandon the reduced clutch plays a large part in determining whether the partial depredation event results in a successful nesting attempt. We found that mallard and gadwall females abandoned partially depredated nests about one-third of the time (Table 1). Whether females stay with or abandon nests depends on the remaining clutch size and stage in incubation—females tend to abandon small clutches and nests partially depredated early in incubation and stay with larger and older clutches (Armstrong and Robertson 1988, Ackerman et al. 2003). However, most females stayed with partially depredated clutches, and these nests often were successful (Table 1). Egg success of nests that were partially depredated also was high (Fig. 4). Contrary to Hall (1987), we found no evidence that success of the remaining eggs in partially depredated nests was lower than that of eggs in intact nests for mallards or gadwalls. In total, over one-fifth of all the ducklings produced in the Suisun Marsh from 1998 to 2000 came from partially depredated nests (Table 3).

Understanding the predators and predator behaviors involved with partial clutch depredation could help managers develop more effective management strategies. Partially depredated nests had either eggs missing or eggshell evidence remaining near the nest site, and the number of eggs lost from these types of nests differed. Fewer eggs were lost from nests in which the only evidence of partial clutch depredation was missing eggs than from nests with eggshell evidence of depredation (Table 2). This difference in egg loss may be due to different predators or predator behaviors (e.g., satiation, foraging mode).

We suspect that striped skunks caused most partial clutch losses, although determining the identities of nest predators from eggshell remains is difficult (Larivière and Messier 1997, Larivière 1999). McLandress et al. (1996) suggested that striped skunks were a major predator of duck nests in the Suisun Marsh. Additionally, using remote cameras and track-plates, Ackerman (2002*a*) found that striped skunks were the most active predators within the nesting fields during the 2000 breeding season. Striped skunks often become satiated after eating an average-sized duck clutch (Nams 1997), and frequently do not finish eating an entire clutch (Larivière and Messier 1997, Greenwood et al. 1999). Larivière and Messier (1997) found that striped skunks consumed only 3.4 ± 1.3 eggs from natural nests and 3.7 ± 1.7 eggs from simulated nests during the initial depredation event. In our study, partial clutch depredation resulted in egg losses of similar magnitude (about 3 eggs per nest; Table 1), suggesting that striped skunks were a principle cause of partial clutch loss.

Other common predators of duck nests in the Suisun Marsh include coyotes (*Canis latrans*), raccoons (*Procyon lotor*), gopher snakes (*Pituophis melanoleucus*), and common ravens (*Corvus corax*; J. T. Ackerman, unpublished data). Large gopher snakes are especially common and have been seen within duck nests, presumably to consume eggs (J. T. Ackerman, personal observation). We suspect that gopher snakes and ravens were responsible for some of the partial clutch depredations resulting in missing eggs and larger remaining clutch sizes, although mammalian predators or females removing eggshells also may have been responsible (Larivière and Walton 1998, Larivière 1999). Studies using infrared video camera systems deployed at nest sites (e.g., Pietz and Granfors 2000) could provide more detailed information on predator behavior at the nest site and help determine why clutches often are partially depredated.

MANAGEMENT IMPLICATIONS

Potential management strategies for partial clutch depredation will depend on understanding the predator community involved, the behavior of predators at the nest site, and how females decide to stay with or abandon a partially reduced clutch. Predators and predator behaviors that only partially consume a clutch may not influence duckling production to the same extent as predators and behaviors that completely destroy a nest, and, therefore, may warrant less management attention. In addition, development of techniques that could reduce the number of eggs being taken from nests could increase nest success because females often will stay with nests following small clutch losses (Armstrong and Robertson 1988, Ackerman et al. 2003). For example, satiating predators with supplemental (Crabtree and Wolfe 1988, Greenwood et al. 1998) or alternate prey (Ackerman 2002*a*) might reduce the number of eggs being consumed during a depredation event.

Understanding partial clutch depredation also may be useful when considering the costs and benefits of predator control. Several of the species that partially depredate clutches may be the least likely to be reduced by predator-control strategies. For example, predator removal and exclosures (e.g., fences, nesting islands) typically target large terrestrial mammalian species, whereas other important duck nest predators such as birds, snakes, and rodents often are able to access nests inside management areas (Lokemoen et al. 1982, Choromanski-Norris et al. 1989, Greenwood et al. 1990). Although nesting densities and nest success may increase within predator-management areas, egg success often is not reported (e.g., Greenwood 1986, Greenwood et al. 1990, Sargeant et al. 1995, Garrettson and Rohwer 2001), and the hatching clutch size may be smaller due to partial clutch depredations by nontargeted egg predators (e.g., Lokemoen et al. 1982). Hence, the benefit of these management strategies may not be as great as previously thought. On the other hand, some managers feel that predator-control efforts are not worthwhile because of compensatory nest depredation by nontargeted predator species. However, if these nontargeted predators depredate clutches partially rather than completely, then predator control still may be worthwhile because a substantial number of ducklings are produced from partially depredated nests. Examining the contribution of partially depredated nests to duckling production may allow managers to more fully evaluate predator-management alternatives.

We recommend that an estimate of egg success, in addition to nest success, be incorporated to accurately assess duckling production. Our results indicate that failure to do so may cause managers to overestimate mallard duckling production by 10%. Future research also should evaluate the prevalence of partial clutch depredation in other important waterfowl production areas.

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LITERATURE CITED

ACKERMAN, J. T. 2002*a*. Of mice and mallards: positive indirect effects of coexisting prey on waterfowl nest success. Oikos 99:469–480.

———. 2002*b*. From individuals to populations: the direct and indirect effects of predation on waterfowl nest success. Dissertation, University of California-Davis, Davis, California, USA.

———, J. M. EADIE, G. S. YARRIS, D. L. LOUGHMAN, AND M. R. MCLANDRESS. 2003. Cues for investment: nest desertion in response to partial clutch depredation in dabbling ducks. Animal Behaviour: in press.

AFTON, A. D., AND S. L. PAULUS. 1992. Incubation and brood care. Pages 62–109 *in* B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu, editors. Ecology and management of breeding waterfowl. University of Minnesota Press, Minneapolis, Minnesota, USA.

ARMSTRONG, T., AND R. J. ROBERTSON. 1988. Parental investment based on clutch value: nest desertion in response to partial clutch loss in dabbling ducks. Animal Behaviour 36:941–943.

BYERS, S. M. 1974. Predator–prey relationships on an Iowa waterfowl nesting area. Transactions of the North American Wildlife and Natural Resources Conference 39:223–229.

CALDWELL, P. J., AND G. W. CORNWELL. 1975. Incubation behavior and temperatures of the mallard duck. Auk 92:706–731.

CHOATE, J. S. 1967. Factors influencing nesting success of eiders in Penobscot Bay, Maine. Journal of Wildlife Management 31:769–777.

CHOROMANSKI-NORRIS, J., E. K. FRITZELL, AND A. B. SARGEANT. 1989. Movements and habitat use of Franklin's ground squirrels in duck-nesting habitat. Journal of Wildlife Management 53:324–331.

CLARK, R. G., AND T. D. NUDDS. 1991. Habitat patch size and duck nest success: the crucial experiments have not been performed. Wildlife Society Bulletin 19:534–543.

COWARDIN, L. M., D. S. GILMER, AND C. W. SHAIFFER. 1985. Mallard recruitment in the agricultural environment of North Dakota. Wildlife Monographs 92.

CRABTREE, R. L., AND M. L. WOLFE. 1988. Effects of alternative prey on skunk predation of waterfowl nests. Wildlife Society Bulletin 16:163–169.

EISENHAUER, D. I., AND C. M. KIRKPATRICK. 1977. Ecology of the emperor goose in Alaska. Wildlife Monographs 57.

GARRETTSON, P. R., AND F. C. ROHWER. 2001. Effects of mammalian predator removal on production of upland-nesting ducks in North Dakota. Journal of Wildlife Management 65:398–405.

GLOUTNEY, M. L., R. G. CLARK, A. D. AFTON, AND G. J. HUFF. 1993. Timing of nest searches for upland nesting waterfowl. Journal of Wildlife Management 57:597–601.

GRAND, J. B., AND P. L. FLINT. 1997. Productivity of nesting spectacled eiders on the lower Kashunuk River, Alaska. Condor 99:926–932.

GREENWOOD, R. J. 1986. Influence of striped skunk removal on upland duck nest success in North Dakota. Wildlife Society Bulletin 14:6–11.

———, P. M. ARNOLD, AND B. G. MCGUIRE. 1990. Protecting duck nests from mammalian predators with fences, traps, and a toxicant. Wildlife Society Bulletin 18:75–82.

———, D. G. PIETRUSZEWSKI, AND R. D. CRAWFORD. 1998. Effects of food supplementation on depredation of duck nests in upland habitat. Wildlife Society Bulletin 26:219–226.

———, A. B. SARGEANT, D. H. JOHNSON, L. M. COWARDIN, AND T. L. SHAFFER. 1995. Factors associated with duck nest success in the prairie pothole region of Canada. Wildlife Monographs 128.

———, ———, J. L. PIEHL, D. A. BUHL, AND B. A. HANSON. 1999. Foods and foraging of prairie striped skunks during the avian nesting season. Wildlife Society Bulletin 27:823–832.

HALL, M. R. 1987. Nesting success in mallards after partial clutch loss by predators. Journal of Wildlife Management 51:530–533.

JOHNSON, D. H. 1979. Estimating nest success: the Mayfield method and an alternative. Auk 96:651–661.

———, J. D. NICHOLS, AND M. D. SCHWARTZ. 1992. Population dynamics of breeding waterfowl. Pages 446–485 *in* B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu, editors. Ecology and management of breeding waterfowl. University of Minnesota Press, Minneapolis, Minnesota, USA.

———, A. B. SARGEANT, AND R. J. GREENWOOD. 1989. Importance of individual species of predators on nesting success of ducks in the Canadian Prairie and Pothole Region. Canadian Journal of Zoology 67:291–297.

KLETT, A. T., H. F. DUEBBERT, C. A. FAANES, AND K. F. HIGGINS. 1986. Techniques for studying nest success of ducks in upland habitats in the Prairie Pothole Region. U.S. Fish and Wildlife Service Resource Publication 158.

———, T. L. SHAFFER, AND D. H. JOHNSON. 1988. Duck nest success in the Prairie Pothole Region. Journal of Wildlife Management 52:431–440.

LARIVIÈRE, S. 1999. Reasons why predators cannot be inferred from nest remains. Condor 101:718–721.

———, AND F. MESSIER. 1997. Characteristics of waterfowl nest depredation by the striped skunk, *Mephitis mephitis*: can predators be identified from nest remains? American Midland Naturalist 137:393–396.

———, AND L. R. WALTON. 1998. Eggshell removal by duck hens following partial nest depredation by striped skunk. Prairie Naturalist 30:183–185.

LOKEMOEN, J. T., H. A. DOTY, D. E. SHARP, AND J. E. NEAVILLE. 1982. Electric fences to reduce mammalian predation of waterfowl nests. Wildlife Society Bulletin 10:318–323.

———, AND R. O. WOODWARD. 1993. An assessment of predator barriers and predator control to enhance duck nest success on peninsulas. Wildlife Society Bulletin 21:275–282.

MAYFIELD, H. F. 1961. Nest success calculated from exposure. Wilson Bulletin 73:255–261.

———. 1975. Suggestions for calculating nest success. Wilson Bulletin 87:456–466.

MCKINNON, D. T., AND D. C. DUNCAN. 1999. Effectiveness of dense nesting cover for increasing duck production in Saskatchewan. Journal of Wildlife Management 63:382–389.

MCLANDRESS, M. R., G. S. YARRIS, A. E. H. PERKINS, D. P. CONNELLY, AND D. G. RAVELING. 1996. Nesting biology of California mallards. Journal of Wildlife Management 60:94–107.

NAMS, V. O. 1997. Density-dependent predation by skunks using olfactory search images. Oecologia 110:440–448.

PIETZ, P. J., AND D. A. GRANFORS. 2000. Identifying predators and fates of grassland passerine nests using miniature video cameras. Journal of Wildlife Management 64:71–87.

SARGEANT, A. B., AND D. G. RAVELING. 1992. Mortality during the breeding season. Pages 396–422 *in* B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu, editors. Ecology and management of breeding waterfowl. University of Minnesota Press, Minneapolis, Minnesota, USA.

———, M. A. SOVADA, AND T. L. SHAFFER. 1995. Seasonal predator removal relative to hatch rate of duck nests in waterfowl production areas. Wildlife Society Bulletin 23:507–513.

SOVADA, M. A., A. B. SARGEANT, AND J. W. GRIER. 1995. Differential effects of coyotes and red foxes on duck nest success. Journal of Wildlife Management 59:1–9.

WELLER, M. W. 1956. A simple field candler for waterfowl eggs. Journal of Wildlife Management 20:111–113.

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