Breeding ecology of White-faced Ibis (*Pleagadis chihi*) in the Upper Klamath Basin, California

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During the 1960s and 1970s, White-faced Ibis (Plegadis chihi; AOU 1998) populations declined sharply in North America from negative effects of organochlorine pesticides and extensive wetland losses from drought and drainage (Ryder 1967, King et al. 1980). White-faced Ibis have a limited number of consistent breeding sites (Sharp 1985), and the Great Basin White-faced Ibis population (Earnst et al. 1998) is recognized by the California Department of Fish and Game (CDFG) and the U.S. Fish and Wildlife Service (USFWS) as a species of special concern and a species of management concern, respectively (Remsen 1978, USFWS 1995, L. Comrack, CDFG, personal communication). Within North America, marshes of the Great Basin are considered a stronghold of White-faced Ibis reproduction (Ryder 1967, Ryder and Manry 1994), and the Great Basin White-faced Ibis population's nesting biology in this region has been well studied (Kotter 1970, Kaneko 1972, Capen 1977, Alford 1978, Steele 1980, Henny and Herron 1989, Kelchlin 1994, 1996, 1997, Henny 1997). In contrast, from 1914 to 1986, only small numbers (maximum 12 pairs) nested sporadically in the Klamath Basin of southern Oregon and northeastern California (Grinnell and Miller 1944, Ryder 1967, Booser and Sprunt 1980, Follansbee and Mauser 1994). However, by 1994 on Lower Klamath National Wildlife Refuge (NWR), the White-faced Ibis population had increased dramatically to 3900 pairs (Follansbee and Mauser 1994).

Conservation and management of White-faced Ibis habitat requires comprehensive knowledge of their nesting biology. In 1994, Follansbee and Mauser (1994) monitored 30 White-faced Ibis nests on Lower Klamath NWR and observed 96.6% apparent nest success (n = 115), 82% hatchability, 97% whole and partial brood survival, and 2.39 fledglings per successful nest. Mayfield estimates of nest survival were 79.1% during the laying and incubation period and 95% during the nesting period. Overall nest success as estimated by the Mayfield method was 75.4%. Our estimates of nest success are some of the highest reported anywhere in the literature for White-faced Ibis. Therefore, Lower Klamath NWR may maintain preferred White-faced Ibis breeding habitats in years of otherwise poor habitat conditions across the Intermountain West.

Key words: White-faced Ibis, Plegadis chihi, breeding ecology, wetlands, Klamath Basin, California, nest success.

STUDY AREA

We studied White-faced Ibis from 26 May to 28 July 1995 on Lower Klamath NWR (42°N,
121°45’W), Siskiyou County, California (Fig. 1). Lower Klamath NWR is 1220 m in elevation and contains 19,500 ha of managed permanent and seasonal wetlands, uplands, and barley fields (Mauser et al. 1994).

METHODS

Breeding Population

We located White-faced Ibis colonies by searching for early morning and late evening foraging flights. To estimate the total number of breeding pairs on Lower Klamath NWR, we conducted a single sunrise flyout count at each colony during incubation and early nesting periods. We assumed that during these periods 1 member of the pair would remain on the nest and the other would leave the nesting area to forage (Belknap 1957, Kotter 1970). Therefore, our counts would result in an estimate of breeding pairs. We began each count as soon as we observed birds leaving the colony and terminated it when the 1st birds returned. Because sunrise flyout counts were ineffective at 1 colony (13a), on 20 June 2 observers estimated population size from an aerial overflight.

Nesting Ecology

Within each of the 3 colonies, we randomly selected a sample of 40–45 active nests (containing at least 1 egg) by systematically choosing every 10th nest along a modified zigzag belt transect (Krebs 1989) that included nests from both the center and edge of the colony. White-faced Ibis nests tended to be clustered in patches of emergent vegetation surrounded by water. Thus, to avoid sampling the majority of nests from a small area, we interspersed nest selection by choosing a maximum of 4 nests per patch. We marked nests by attaching colored flagging tape or clothespins to nearby vegetation.

To decrease the possibility of nest abandonment during the egg-laying period, we delayed our 1st colony visit until the majority of nests were being incubated. To avoid thermal stress to eggs and/or chicks (Tyler 1933, Belknap 1957, Kotter 1970, Ryder and Manry 1994), we visited colonies during the morning (0700–1000) or evening (1700–1830) hours unless temperatures were less than 7°C. We made an average of 5 visits per colony from 31 May to 17 July, with an average interval of 6 d between successive visits (range 3–14 d). During each visit we recorded the number and age of eggs and/or nestlings. Incubation stage was estimated by egg flotation (Westerskov 1950), assuming a 22-d incubation period (Bent 1926, Belknap 1957, reviewed in Ryder and Manry 1994), and nestling age was estimated from known hatching dates or from growth and development of feather tracts (Belknap 1957, Kotter 1970, E. Kelchlin, Stillwater NWR, Fallon, NV, personal communication).

We determined the fate of eggs (e.g., missing, hatched, unhatched, or destroyed) by revisiting...
nests 1–5 d after their projected hatching dates. Nestling fate was determined by monitoring nests until they failed or until chicks reached 6–10 d old, in which case we considered them as having “fledged” (i.e., capable of leaving the nest to escape a predator). Nestlings older than 7–10 d are mobile and frequently leave the nest during investigator approach, making it difficult to count them accurately (Frederick et al. 1993, Ryder and Manry 1994). If nests had missing eggs or young, we searched the nest site area thoroughly for remains of eggs or chicks.

For all nests we calculated mean clutch size and nest initiation date (Julian) for each colony. Nest initiation dates were estimated by back-dating from our egg flotation data, assuming a 2-d laying interval (Kotter 1970, reviewed in Ryder and Manry 1994).

Reproductive Success

APPARENT NEST SUCCESS.—We calculated 4 measures of reproductive success for each colony: (1) apparent nest success was the proportion of all nests that hatched at least 1 egg, (2) hatchability was the proportion of eggs that hatched from successful nests (those hatching at least 1 egg), (3) whole brood survival was the proportion of successful nests that fledged at least 1 chick (6–10 d old), (4) partial brood survival was the proportion of chicks reaching 6–10 d of age from nests that fledged at least 1 chick, and (5) fledging success was the mean number of chicks (6–10 d old) fledged per successful nest.

MAYFIELD NEST SUCCESS.—We used the Mayfield (1961, 1975) method to calculate nest success and daily nest survival rates for each colony, with standard errors calculated according to Johnson (1979). We compared daily survival rates among colonies using Z tests (Johnson 1979).

UNSUCCESSFUL NESTS.—For failed nests we distinguished between destroyed nests (at least 1 egg/nestling destroyed by a predator) and 3 categories of abandoned nests: (1) eggs intact but no longer attended by parents, (2) cracked or flattened eggs in the water near the nest, and (3) cracked or flattened eggs in the nest.

Statistical Analyses

Using simple linear regression, we determined whether clutch size varied with nest initiation date. Clutch sizes among colonies were compared using 1-way ANOVA. Because nest initiation data did not meet assumptions of normality and homogeneity of variances (Dowdy and Wearden 1991), we compared nest initiation dates among colonies using nonparametric 1-way ANOVA (Kruskal-Wallis Test; Hintze 1995). Statistical analyses were performed using NCSS (Hintze 1995).

RESULTS

Breeding Population

We located 3 White-faced Ibis colonies on Lower Klamath NWR in 1995 (Fig. 1) with an estimated 2029 breeding pairs (Table 1). Colony 7a was in a 242-ha permanent marsh dominated by early-successional hardstem bulrush (Scirpus acutus; Hickman 1993), colony 8b in a 302-ha permanent marsh characterized by early-successional hardstem bulrush interspersed with common cattail (Typha latifolia; Hickman 1993), and colony 13a in a 1334-ha unit with approximately 800 ha of seasonal marsh habitat dominated by early-successional hardstem bulrush. White-faced Ibis nested exclusively in patches of hardstem bulrush with relatively low stem densities (i.e., water was visible under nests). All 3 colonies included Franklin’s Gulls (Larus pipixcan; AOU 1998) and Forster’s Terns (Sterna forsteri; AOU 1998); colonies 7a and 13a also included Black-crowned Night Herons (Nycticorax nycticorax; AOU 1998), Snowy Egrets (Egretta thula; AOU 1998), and Great Egrets (Casmerodius albus; AOU 1998).

Nesting Ecology

Clutch size averaged 3.16 and did not vary among colonies (F2 = 2.79, P = 0.07; 1-way ANOVA), but mean nest initiation dates varied from 14 (colony 7a) to 31 May (colony 8b; Kruskal-Wallis ANOVA, \( \chi^2 = 87.5, P < 0.0001 \); Table 1). For all colonies combined, clutch size was negatively correlated with Julian nest initiation date (\( y = 7.09 - 0.03x, r = -0.30, n = 124, P = 0.001 \)).

Reproductive Success

APPARENT NEST SUCCESS.—Reproductive success in all colonies averaged 87% apparent nest success, 82% hatchability, 97% whole brood survival, 97% partial brood survival, and 2.39 fledglings per successful nest (Table 2).
MAYFIELD NEST SUCCESS.—Daily nest survival was 0.9850 and did not vary among colonies during the incubation (Z ≤ 0.89, P ≥ 0.38) or nestling periods (Z ≤ 1.57, P ≥ 0.12). Although daily survival rates did not differ between the incubation (DSR = 0.9910 ± 0.0025) and nestling periods (DSR = 0.9940 ± 0.0030; Z = –0.71, P = 0.48), we kept these periods separate for calculating overall Mayfield nest success, which averaged 75% (Table 3).

UNSUCCESSFUL NESTS.—Of 17 nests that failed, 13 were lost during the incubation period (6 destroyed by predators, 7 abandoned), and 4 were lost during the nestling period (3 destroyed by predators, 1 abandoned). Of 8 abandoned nests, 1 was abandoned with eggs intact, 2 had cracked and/or flattened eggs in the water near the nest, 4 had cracked and/or flattened eggs still in the nest, and 1 had a dead flattened chick still in the nest.

DISCUSSION

The reliance of White-faced Ibis at Lower Klamath NWR on hardstem bulrush for nesting was similar to that of White-faced Ibis breeding in the Great Basin (Kaneko 1972, Sharp 1985, Schreur 1987, Henny and Herron 1989, Cornely et al. 1994). Before the 1980s Lower Klamath NWR contained relatively few early-successional emergent marshes because most marsh units were managed as long-term permanent wetlands or seasonal wetlands. In the early 1980s refuge staff began to remove water from seasonal marshes during late spring and early summer to stimulate seed production of moist-soil plants (Fredrickson and Taylor 1982). This resulted in expansion of early-successional emergent plants, particularly thin stands of hardstem bulrush favored by White-faced Ibis.

White-faced Ibis nesting on Lower Klamath NWR in 1995 experienced higher apparent nesting success (87%) than had been reported previously (i.e., ≤69%; Kotter 1970, Kaneko 1972, Capen 1977, Alford 1978, Kelchlin 1994). Follansbee and Mauser (1994) also reported very high apparent nest success (96.6%) for a single White-faced Ibis colony on Lower Klamath NWR during 1994. Although our estimate of hatchability (82%) was lower than that reported for other colonial nesting species (88.6%; Koenig 1982), it was nonetheless higher than that documented in other White-faced Ibis studies (i.e., ≤66%; Kotter 1970, Kaneko 1972, Capen 1977, Alford 1978, Kelchlin 1994). Our overall estimate of 2.39 fledglings (i.e., 6–10 d old) produced per nest was similar to other White-faced Ibis studies. Over a 2-yr period the number of 10-d-old fledglings produced per successful nest ranged from 1.47 to 3.04 in the Carson River Basin, Nevada, and 2.00 to 3.10 in Colorado (Schreur 1987, Kelchlin 1994, 1996). In Utah the minimum number of fledglings (i.e., 7 d old) produced per nest was 0.10 and the maximum was 2.67 (Kotter 1970, Kaneko 1972, Steele 1980). In Nevada an average of 2.54 fledglings (i.e., 7–10 d old) was produced per successful nest (Henny and Herron 1989).

Our Mayfield (1961, 1975) estimate of nest success during the laying and incubation period was 79%, which was lower than our

<table>
<thead>
<tr>
<th>Colony</th>
<th>Number of breeding pairs a</th>
<th>Nest initiation date</th>
<th>Clutch size</th>
<th>Number of nests b</th>
</tr>
</thead>
<tbody>
<tr>
<td>7a</td>
<td>1149</td>
<td>14 May ± 2 (10–20 May)</td>
<td>3.23 ± 0.58 (2–4)</td>
<td>40</td>
</tr>
<tr>
<td>8b</td>
<td>305</td>
<td>31 May ± 4 (26 May–10 June)</td>
<td>2.93 ± 0.93 (1–5)</td>
<td>41</td>
</tr>
<tr>
<td>13a</td>
<td>575</td>
<td>25 May ± 7 (14 May–12 June)</td>
<td>3.30 ± 0.79 (1–5)</td>
<td>45</td>
</tr>
<tr>
<td>Overall</td>
<td>2029</td>
<td>24 May ± 9 (10 May–12 June)</td>
<td>3.16 ± 0.79 (1–5)</td>
<td>126</td>
</tr>
</tbody>
</table>

aEstimated by sunrise flyout counts (colonies 7a, 8b) and aerial census (colony 13a).
bSample size of monitored nests used for nest initiation date and clutch size analyses.
Table 2. Apparent nest success for 3 White-faced Ibis colonies on Lower Klamath National Wildlife Refuge, California, 1995.

<table>
<thead>
<tr>
<th>Colony</th>
<th>Percent nest successa (n)</th>
<th>Percent hatchb (n)</th>
<th>Percent whole brood survival c (n)</th>
<th>Percent partial brood survival d (n)</th>
<th>Fledging success (mean ± s) (n)</th>
</tr>
</thead>
<tbody>
<tr>
<td>7a</td>
<td>91 (35)</td>
<td>86 (104)</td>
<td>92 (13)</td>
<td>97 (33)</td>
<td>2.46 ± 0.97 (13)</td>
</tr>
<tr>
<td>8b</td>
<td>88 (40)</td>
<td>84 (107)</td>
<td>100 (30)</td>
<td>96 (74)</td>
<td>2.37 ± 0.89 (30)</td>
</tr>
<tr>
<td>13a</td>
<td>83 (40)</td>
<td>77 (110)</td>
<td>96 (23)</td>
<td>98 (56)</td>
<td>2.39 ± 1.23 (23)</td>
</tr>
<tr>
<td>Overall</td>
<td>87 (115)</td>
<td>82 (321)</td>
<td>97 (66)</td>
<td>97 (163)</td>
<td>2.39 ± 1.02 (66)</td>
</tr>
</tbody>
</table>

aNest success was the proportion of all nests that hatched at least 1 egg.
bTotal number of nests on which calculations were based.
cPercent hatchability, defined as the proportion of eggs that hatched from successful nests.
dTotal number of eggs on which calculations were based.
eTotal number of chicks on which calculations were based.
fFledging success was the mean number of chicks (6–10 d old) fledged per successful nest.


<table>
<thead>
<tr>
<th>Colony</th>
<th>Percent nest survivalc</th>
<th>Percent hatchb</th>
<th>Percent nestling survivald</th>
<th>Overall nest success e</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Laying/incubation period</td>
<td>Nesting period</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Nests</td>
<td>Exposure days</td>
<td>Losses</td>
<td>Daily survival</td>
</tr>
<tr>
<td>7a</td>
<td>40</td>
<td>445.5</td>
<td>3</td>
<td>0.9933</td>
</tr>
<tr>
<td>8b</td>
<td>41</td>
<td>349.5</td>
<td>5</td>
<td>0.9857</td>
</tr>
<tr>
<td>13a</td>
<td>45</td>
<td>652.0</td>
<td>5</td>
<td>0.9923</td>
</tr>
<tr>
<td>Total</td>
<td>126</td>
<td>1447.0</td>
<td>13</td>
<td>0.9910</td>
</tr>
</tbody>
</table>

aLaying/incubation period included laying period of 4 d and incubation period of 22 d.
bStandard error (s) calculated following Johnson (1979).
cPercent nest survival for the laying/incubation period calculated as (daily survival rate for laying + incubation)0.5 * 100 (Johnson 1979).
dPercent nestling survival for nestling period calculated as (daily survival rate)8 * 100 (Johnson 1979).
eThe product of percent nest survival * percent nestling survival.
estimate of 87% apparent nest success. The Mayfield method accounts for nests that were destroyed before they were found and is usually a less biased estimator of nest success (Johnson 1979, Hensler and Nichols 1981). Our Mayfield estimates of nest success during the laying and incubation period (79.1%) and the nestling period (95.3%) are similar to those reported by Kelchlin (1996; 79.9% and 95.0%, respectively) and higher than those documented by Kelchlin (1997; incubation = 63.2%, nestling = 89.3%). Our Mayfield estimate of overall nest success (75.4%) is almost identical to the 75.9% Mayfield estimate of overall nest success documented by Kelchlin (1996) but higher than the 56.4% overall Mayfield nest success reported in 1996 by Kelchlin (1997).

Clutch size declined later in the breeding season, a pattern well documented in other White-faced Ibis studies (Alford 1978, Steele 1980, Henny and Herron 1989) and among birds in general (Lack 1968).

We suspect the high nest success and fledgling rate for White-faced Ibis on Lower Klamath NWR can be attributed to a combination of (1) sturdy and favorable nesting habitat (hardstem bulrush), (2) accessible foraging habitats within the refuge and adjacent private cattle pastures that contained abundant resources (primarily earthworms) throughout the nesting season, (3) colonies that remained flooded throughout the nesting period, reducing accessibility by mammalian predators, (4) low densities of Franklin’s Gulls and other potential avian predators, and (5) a relatively favorable climate during the nesting season.

One explanation for the rapid increase in White-faced Ibis breeding populations on Lower Klamath NWR is the expansion of favorable nesting and foraging habitat brought about by previously described changes in habitat management. In addition, the increase may be due in part to immigration of White-faced Ibis from the Great Salt Lake marshes, which were drastically affected by flooding from 1982 through 1985 when traditional colonies were reduced by 80% (Ivey et al. 1988). Finally, the increased breeding populations on Lower Klamath NWR may have included White-faced Ibis dispersing from main breeding colonies in northwestern Nevada (1985–1994 breeding pair average = 2373) during drought conditions in 1991 and 1992 when, respectively, 0 and 315 breeding White-faced Ibis were reported (W. Henry, Stillwater NWR, Fallon, NV, personal communication).

Within the Intermountain West, White-faced Ibis nesting locations can vary considerably among years, with certain sites being used repeatedly while others are used only intermittently (Ryder 1967). Ryder (1967) suggested that this nomadic nesting pattern may be associated with annual fluctuations in hydrology of wetlands where White-faced Ibis nest. Indeed, in years of hydrologic extremes (i.e., drought or flooding), limitation of high-quality breeding habitats would increase the importance of areas with suitable wetlands. Historically, Lower Klamath NWR has received a relatively stable water supply, and so some wetlands can be managed for early-successional hardstem bulrush while others are managed traditionally for breeding and migrating waterfowl. Therefore, Lower Klamath NWR may maintain preferred White-faced Ibis breeding habitats in years of otherwise poor habitat conditions across the Intermountain West.

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