ECOLOGY OF BREEDING WHITE-FACED IBIS ON LOWER KLAMATH NATIONAL WILDLIFE REFUGE, CALIFORNIA
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Abstract - The conservation and management of breeding White-faced Ibis (*Plegadis chihi*), a state and federally listed species of special management concern, requires comprehensive knowledge of the species' nesting ecology. We studied the ecology of breeding White-faced Ibis from May through August 1995 on Lower Klamath National Wildlife Refuge (NWR) and surrounding private agricultural lands of northern California and southern Oregon. On Lower Klamath NWR we monitored the breeding success of 126 nests located in four colonies. Colony sizes ranged from 12 to 1,149 pairs, with an estimated 2,041 total pairs of breeding ibises nesting exclusively in early successional hardstem bulrush (*Scirpus acutus*). Nest initiation dates ranged from 10 May to 28 June and mean clutch size was 3.14. Overall reproductive success was high, averaging 85% nest success during the incubation period (n = 119), 82% hatchability, 97% whole and partial brood survival, and 2.06 fledglings produced per nest. The Mayfield estimate of nest success was 79.1% during the incubation period (n = 126), and 95% during the nestling period (n = 113). We observed up to 84% of the breeding population traveling north of the refuge to forage on private agricultural lands. In agricultural habitats outside of the refuge, foraging ibis preferred flooded grazed cattle pasture. Although adult ibis were significantly more efficient at foraging in wetlands than were juveniles, the two age classes were equally proficient at foraging in pasturelands. Our apparent nest success estimates (85%) are some of the highest reported anywhere in the literature for White-faced Ibis. Moreover, livestock pastures offered valuable foraging habitats to breeding ibis throughout the nesting cycle. We suggest that among breeding localities within the Great Basin, Lower Klamath NWR has great potential to become a significant breeding stronghold for White-faced Ibis in the future.

During the 1960's and 1970's, White-faced Ibis (*Plegadis chihi*) populations declined sharply in North America due to negative effects of organochlorine pesticides and extensive wetland losses from drought and drainage (Ryder 1967, King et. al. 1980). In the last two decades, however, nesting populations and nesting colony numbers have increased, which can be partly attributed to enhanced reproductive success from banning DDT and other pesticides, as well as improved management of breeding habitat (Ryder and Manry 1994). Nevertheless, because White-faced Ibis still have a limited number of consistent breeding sites with uncertain status and low population numbers (Sharp 1985), the species is still recognized by the California Department of Fish and Game (CDFG) and the U.S. Fish and Wildlife Service (USFWS) as a bird Species of Special Concern and a Species of Management Concern, respectively (L. Comrack, CDFG, pers comm., USFWS 1995).

The White-faced Ibis has a disjunct breeding range in the New World, occurring in southern South America and in North America west of the Mississippi (A.O.U. 1983). Within North America, the marshes of the Great Basin (e.g. Utah, Nevada, Oregon) have long been considered the stronghold of ibis reproduction (Ryder 1967, Ryder and Manry 1994). In contrast to other geographic areas, the nesting biology of Great Basin White-faced Ibises has been well studied (Kotter 1970, Kaneko 1972, Capen 1977, Alford 1978, Steele 1980, 1984, Henny and Herron 1989, Kelchlin 1994). Within northeastern California, on the western edge of the Great Basin, breeding populations of White-faced Ibis have historically been few and transient.

Prior to the 1980's, White-faced Ibis were considered a rarity within the Klamath Basin of southern Oregon and northeastern California (Booser and Sprunt 1980). In 1914, ibis were suspected of breeding on Lower Klamath Lake (Grinnell and Miller 1944), but it wasn't until 1959 that four nests were reported at Tule Lake National Wildlife Refuge (NWR). In 1965, an estimated ten pairs bred there (Ryder 1967). Yet in 1966, only two nesting pairs of White-faced Ibis were found in the entire Klamath Basin (Booser and Sprunt 1980). In 1986, twelve nests were again found on Lower Klamath NWR (Follansbee and Mauser 1994). Since that time the White-faced Ibis breeding population on Lower Klamath NWR has dramatically increased to an estimated 3,900 pairs in 1994 (Follansbee and Mauser 1994).

Conservation and management of breeding White-faced Ibises requires comprehensive knowledge of their life history requirements during the entire nesting cycle. The Klamath Basin NWR staff is presently developing a habitat management plan for the Lower Klamath NWR which requires data on White-faced Ibis breeding ecology to gain greater insight on the ecological requirements of the species and to integrate White-faced Ibis habitat needs with traditional refuge management. In 1994, Follansbee and Mauser conducted a pilot study of the ecology of breeding White-faced Ibis on Lower Klamath NWR. Reproductive data from this preliminary study indicated the highest estimated apparent nest success for the incubation period (96.6%; n = 30 nests) reported anywhere in the literature. The purpose of our study was twofold: to verify the high estimated breeding success of White-faced Ibis on Lower Klamath NWR (Follansbee and Mauser 1994) by further investigating the nesting biology of a more representative sample of nests among all active colonies, and secondly, to investigate the foraging ecology of ibis. Specifically, our objectives were to: 1) describe habitat characteristics of colony wetlands and to estimate the breeding population size of all colonies, 2) collect reproductive data (nest initiation date and clutch size), estimate the nest success, and describe the nest-site habitat characteristics for a sample of White-faced Ibis nests, 3) estimate the percentage of the breeding population which travels off the refuge to forage, 4) collect habitat availability data so that inferences concerning habitat selection can be made, and 5) estimate adult and juvenile foraging efficiencies.

STUDY AREA AND METHODS

We studied White-faced Ibis (hereafter "ibis") from May to August 1995 on Lower Klamath NWR located in Siskiyou County, California (Figure 1). Lower Klamath NWR is part of the Klamath Basin NWR complex within the Klamath Basin, 25 km south of Klamath Falls, Oregon. The refuge is at an elevation of 1,220 m and is comprised of 19,500 ha of permanent and seasonal wetlands, uplands, barley fields, and a network of water delivery systems (Mauser et al. 1994).

We located all ibis colonies (colony "3a", "7a", "8b", and "13a") on Lower Klamath NWR by searching for large skeins of ibis within refuge wetlands and by finding the geographic origin of early morning and late evening foraging flights (Follansbee and Mauser 1994). Ibis leave the colony at first light to go forage (the "sunrise flyout," D. Mauser, pers. obs.). To estimate the number of breeding

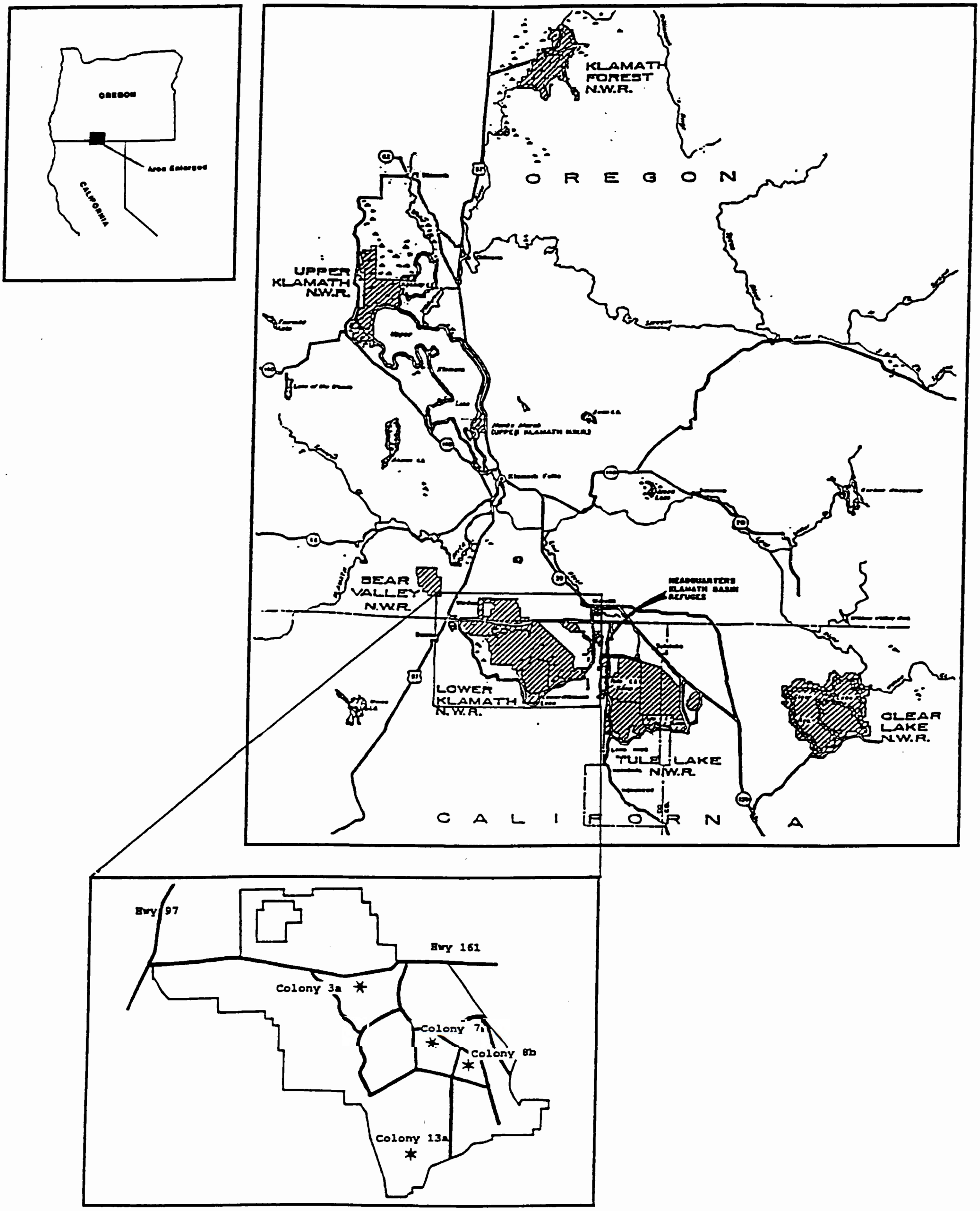

Figure 1. Location of the four White-faced Ibis colonies on Lower Klamath NWR (*), within the Klamath Basin study area of northern California and southern Oregon, 1995.

ibis (i.e. colony size and number of nests) we took advantage of this behavior by conducting flyout counts at sunrise during the incubation and early nestling period (Follansbee and Mauser 1994). Each sunrise flyout count was performed by a single observer strategically located near the colony prior to first light. We began each count as soon as we observed birds leaving the colony and terminated it when birds began re-entering the colony. We assumed that one adult attended the nest while the other left the colony to forage (Follansbee and Mauser 1994), so we doubled each flyout count to obtain an estimate of total number of breeding individuals. Despite hundreds of ibis observed in colony 13a during daytime nest checking visits, repeated sunrise flyout counts yielded numbers (i.e. less than 40 birds) that were incongruous with what we had observed. We therefore conducted one aerial survey with two observers from a Cessna 185 airplane to obtain a more reliable estimate of the number of breeding pairs in colony 13a.

We monitored the reproductive success for a sample of ibis within each of the four colonies (see Figure 1). We measured reproductive success of each colony by conducting regular visits to overwater nests marked with surveyor's flagging and/or colored close pins attached on vegetation above and within one meter of each nest. For each colony, we selected a sample of nests by systematically choosing the nth (a randomly chosen number between one and ten) nest along a modified (zigzag) belt transect (Krebs 1989) which allowed for a more representative survey of nests both within the colony center and along the colony edge. Since ibis nests tended to be clustered in patches of vegetation within colonies, we interspersed nest selection within each colony by choosing a maximum of only four nests per vegetative patch.

We minimized time spent in colonies and the frequency of our visits because human disturbance can cause partial or total nest abandonment (Blaker 1969, Ryder and Manry 1994). In addition, to reduce the amount of human activity and noise in the colony, visits to each colony were usually performed by only one observer. Because unattended eggs and/or chicks are susceptible to chilling or overheating (Tyler 1933, Belknap 1957, Kotter 1970), we usually visited colonies during morning (e.g. 0700-1000) or evening (e.g. 1700-1830) hours, unless temperatures remained cool during mid-day. We made an average of 5 visits per colony from 31 May to 17 July, and the average interval between successive visits was six days (SD = 3.0, range 3-14 days).

To minimize the possibility of abandonment during laying, we delayed our first colony visit until the majority of nests were being incubated. During each colony visit we recorded: 1) date; 2) time; 3) nest contents (i.e. number of eggs and/or nestlings); 4) incubation stage [estimated by egg floatation (Westerkov 1950) assuming a 22 day incubation period (Dawson 1923, Bent 1926, Belknap 1957, Ryder and Manry 1994)]; and 5) nestling age [estimated by a growth and development chart using feather tract development (based on Belknap 1957, Kotter 1970, and E. Kelchlin, pers. comm.) and calibrated by the known nest hatching date].

We determined the fate of eggs (e.g. hatched, unhatched, or destroyed) by revisiting nests as close to one day after hatching as possible. However, because nesting within colonies was highly asynchronous, we checked some nests up to five days after the expected hatch date to maximize nest data obtained per colony visit. Survival estimates of nestlings beyond 7-10 days old are often unreliable because nestlings become very mobile and difficult to count accurately, especially in dense nesting vegetation such as hardstem bulrush (Frederick et al. 1993, Follansbee and Mauser 1994, Ryder and Manry 1994). Therefore, to determine fledgling fate, we monitored nests until they failed or until chicks reached 6-10 days old, in which case we considered them as having "fledged" (i.e. capable of leaving the nest to escape a predator). For marked nests with missing eggs and/or young nestlings, we vigorously searched the nest-site area for evidence of missing eggs or chicks.

We described nesting habitat at each monitored nest-site by measuring nine site characteristics during the laying and incubation period (Table 1). In addition, for colonies we recorded several overall colony characteristics: size of wetland (ha), wetland type (seasonal or permanent), dominant species of vegetation and other nesting birds. Nest-site and colony characteristics were not measured for colony 3a.

We calculated average clutch size and mean nest initiation date (Julian) for all colonies. We estimated nest initiation dates by back-dating from the estimated nest age, assuming a 22 day incubation period (Dawson 1923, Bent 1926, Belknap 1957, Ryder and Manry 1994) and a four day laying period [for a modal clutch size of three (Ryder and Manry 1994) with one egg laid every other day (Kotter 1970)].

We calculated four measures of reproductive success (apparent method) for all colonies. We defined nest success (for the incubation period) as the proportion of nests that hatched at least one egg (Johnson, 1979). We defined hatchability as the proportion of eggs that hatched from

Table 1. List of nest site variables used to describe White-faced Ibis nests on Lower Klamath National Wildlife Refuge, California, 1995.

Measurement (abbreviation)	Description
1. Nest water depth[a] (NSWD)	Measured as water depth directly at the nest (± 1 cm).
2. Vegetation height[a] (VEGH)	Height of vegetation surrounding nest, measured from vegetation base to top of vegetation (± 1 cm).
3. % dead vegetation[b] (DVEG)	Percent dead vegetation within a 1m radius surrounding nest, excluding nesting material.
4. Nest height above water[a] (NHAW)	Distance from water surface to middle of eggs (± 1 cm).
5. Patch size[b] (PASI)	Estimated vegetative patch size of hardstem bulrush (*Scirpus acutus*) where nesting occurred (± 1 m^2).
6. Patch edge[a] (NDPE)	Estimated as the distance from nest cup to patch edge (± 1 cm).
7. Colony edge[b] (NDCE)	Estimated distance from nest cup to nearest edge (i.e. outer boundary) of colony (± 1 m).
8. Nests/patch[b] (NSPA)	Estimated number of ibis nests per patch.
9. Nesting vegetation[b] (NEVG)	The species of vegetation used for nesting.

[a] Measured by calibrated wooden measuring stake (cm).
[b] Ocular estimate.

successful nests. We expressed whole brood survival as the proportion of successful nests (those hatching at least one egg) that fledged at least one chick (6-10 days old). We defined partial brood survival as the number of chicks reaching 6-10 days of age for nests that fledged at least one chick divided by the total number of chicks hatched. We calculated the mean number of "fledglings" (i.e. 6-10 days old) produced per nest as: (number of breeding pairs) * (clutch size) * (nest success) * (hatchability) * (whole brood survival) * (partial brood survival).

We calculated nest success (during the incubation and nestling periods) for colonies 7a, 8b, and 13a using Mayfield's (1961, 1975) method with standard errors calculated according to Johnson (1979). For failed nests, we distinguished between destroyed nests (at least one egg/nestling destroyed by a predator), and three categories of abandoned nests: 1) eggs intact but no longer attended by parents; 2) eggs in water near nest cracked and/or flattened; and 3) eggs in nest cracked and/or flattened. For nests that hatched, we defined the nestling period to be eight days, after which time we considered the nests successfully fledged. We did not include colony 3a nests in the combined (all monitored nests) analysis because of the small amount of information yielded (n = 4 nests, with three of the nests found during the pipping stage).

To estimate the percentage of the breeding population which traveled from Lower Klamath NWR colony sites to forage on private agricultural lands within the Klamath Basin we conducted six counts of ibis traversing at sunrise to these agricultural lands on: 5 June, 25 June, 29 June, 4 July, 18 July, and 4 August. Flyout counts were conducted by one observer positioned prior to first light at the northern main entrance to Lower Klamath NWR. Counts began when the first ibis flock was observed flying north of the refuge border, and ended fifty minutes later.

To determine habitat availability and habitat utilization of foraging ibis on private agricultural lands within the Klamath Basin, we established one habitat utilization transect (hereafter "HUT") which sampled the majority of habitat types available in the Klamath Basin (Follansbee and Mauser 1994). The HUT was located north and northeast of Lower Klamath NWR and was approximately 152 kilometers long, following a pre-determined route (Figure 2). From 9 June to 4 August, we surveyed the HUT for foraging ibis on a weekly basis for ten weeks by automobile with the aid of binoculars and a spotting scope. On each survey occasion, we estimated the number of irrigated fields

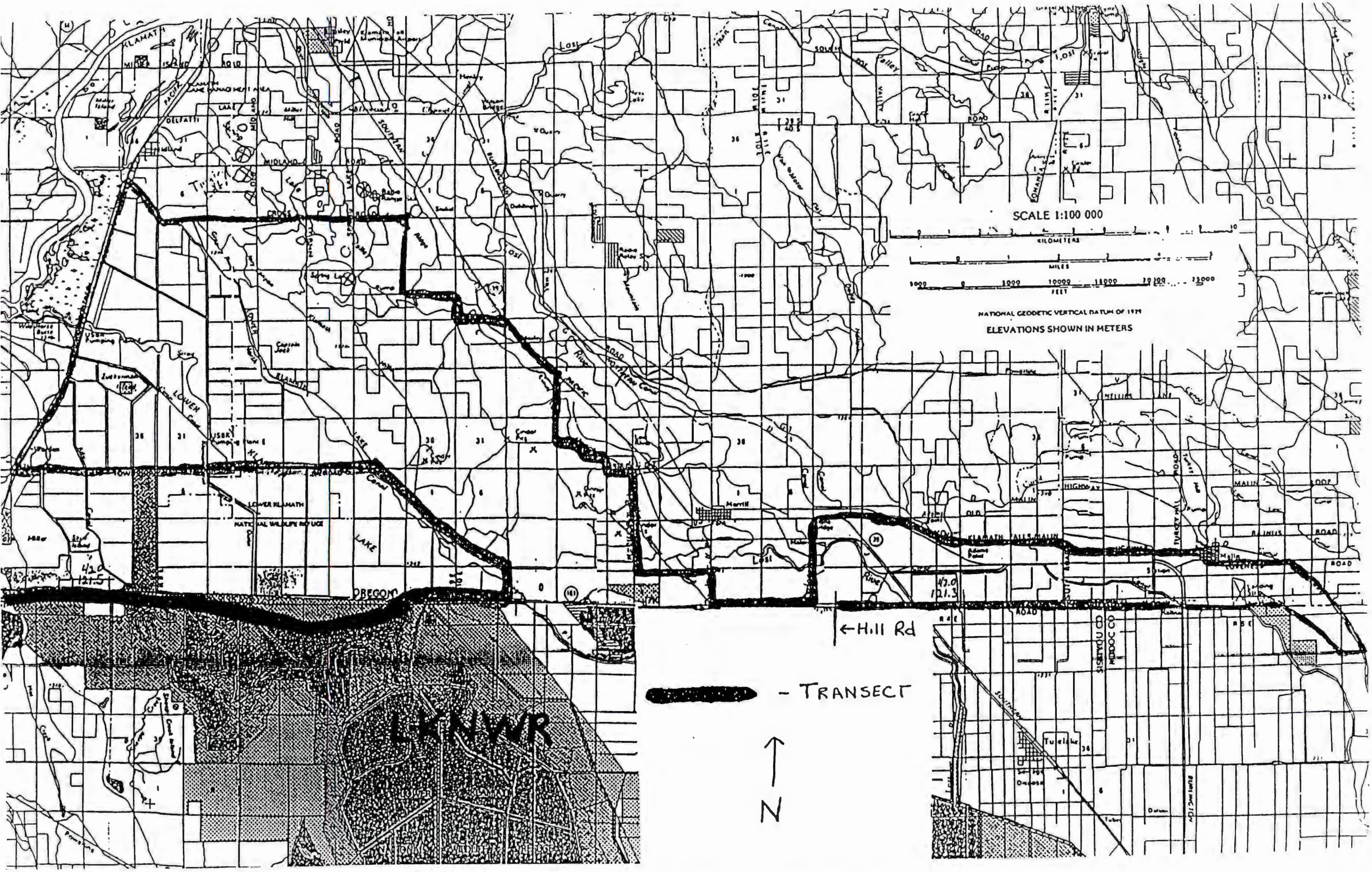

Figure 2. Map of the habitat utilization transect (HUT) used to determine field type preference of White-faced Ibis on private agricultural lands within the Klamath Basin of northern California and southern Oregon (from Follansbee and Mauser 1994).

available on the transect. For each foraging ibis flock encountered on a HUT, we recorded the following data: 1) numbers of birds, 2) field type (grazed pasture, ungrazed pasture, alfalfa, sugar beet, onion, small grains, fallow), 3) presence or absence of standing water, 4) vegetation height (estimated with cm stake placed in the field or estimated by relationship of vegetation to foraging ibises tarsometatarsus), 5) flock distance from road (estimated visually to nearest 10 m), and 6) flock location, which was mapped on USGS topographical maps. In addition, in late July, we recorded the total number of field types available on the entire transect.

From 16 July to 5 August we estimated the foraging efficiency of juveniles and adults in wetland and agricultural habitats surrounding Lower Klamath NWR. We opportunistically located foraging ibis flocks with both juvenile and adult birds present. Juveniles and adults were positively identified based on plumage and bill color differences (Bent 1926). To estimate ibis foraging efficiency and to compare efficiency among age classes we randomly chose one juvenile and one adult within each located flock. For each foraging bird we recorded the following habitat data: 1) field type (see above) and 2) amount of water present, categorized as: a) no water,

b) water depth less than half the length of the tarsometatarsus (i.e. water below the "knee"), or c) water depth greater than half the length of the tarsometatarsus (i.e. water above the "knee"). Additionally, during a one minute observation period we quantified three aspects of foraging behavior for each bird: 3) the number of feeding attempts (judged by the return of an ibises' head to a horizontal position and/or removal of bill from the substrate or its surface), 4) number of foraging successes (judged by swallowing motions) and 5) foraging method(s), categorized as either probe, peck, "scissor", or any combination of these maneuvers. We define a "probe" as an individual foraging on food items below the substrate surface, and a "peck" as an individual foraging on food items above or upon the substrate surface (Martin and Bateson 1990). We observed the "scissor" method (the rapid opening and closing of the upper and lower mandibles resembling scissors opening and closing), in aquatic habitats only. The "scissor" method is equivalent to Belknap's (1957:16) description of the "stationary" method of foraging.

We used simple linear regression (Hintze 1995, Dowdy and Weardon 1991) to determine if clutch size was associated with nest initiation date. We also used simple linear regression to determine if flock size was associated with distance from road and if flock size was related to vegetation height (Hintze 1995, Dowdy and Weardon 1991). We used a paired T-test to determine if adults differed from juveniles in foraging efficiency (Hintze 1995, Dowdy and Weardon 1991).

RESULTS

Nest-site characteristics

All ibis nests were found in patches of hardstem bulrush with relatively low stem densities (i.e. water was visible under nests). While nest site characteristics, nest height above water (NSWD), vegetation height (VEGH), and percent dead vegetation surrounding the nest (DVEG) varied very little among colonies, mean nest height (NHAW) of colony 7a was roughly three times that of colony 8b (Table 2). Colony 13a had on average a 78% larger patch size (PASI) and 25% more nests per patch (NSPA) than colony 8b (Table 2). Nest distance from patch edge (NDPE) for colony 8b was 6.5% less than colony 13a and nest distance to the colony edge (NDCE) for colony 7a was 4% greater than colony 8b (Table 2).

Table 2. Nest site characteristics used to describe nesting habitat for all colonies of breeding White-faced Ibis on Lower Klamath National Wildlife Refuge (LKNWR), California, 1995.

Nest site variable[b]	Overall[a] (n = 126)			Colony 7a (n = 40)			Colony 8b (n = 41)			Colony 13a (n = 45)		
	Mean	SD	Range	Mean	SD	Range	Mean	SD	Range	Mean	SD	Range
NSWD[c] (cm)	59	14	(36-81)	47	6	(36-56)	76	5	(64-81)	56	8	(41-74)
VEGH[c] (cm)	147	52	(0-229)	179	51	(25-229)	120	39	(51-178)	143	52	(0-229)
DVEG[c] (%)	45	31	(1-100)	31	28	(1-90)	38	24	(1-80)	67	28	(2-100)
NHAW[c] (cm)	47	34	(8-152)	71	42	(25-152)	21	10	(8-51)	51	24	(8-103)
PASI[c] (m^2)	139	272	(1-1750)	87	91	(9-335)	4	3	(1-11)	313	394	(1-1750)
NDPE[c] (cm)	83	116	(0-610)	96	58	(15-183)	22	13	(5-61)	147	178	(0-610)
NDCE[c] (m)	46	48	(0-220)	95	64	(0-220)	23	19	(0-66)	41	32	(0-110)
NSPA[c]	14	20	(1-75)	18	21	(1-75)	1	< 1	(1-2)	25	23	(1-70)

[a] Overall total for all monitored nests on LKNWR (i.e. includes colonies 3a, 7a, 8b, and 13a).
[b] Abbreviations of nest site variable names are defined in Table 1.
[c] All measurements rounded to the nearest whole unit.

Estimated population size

We estimated that 2,041 pairs of ibises bred at Lower Klamath NWR in 1995. The number of breeding pairs for each colony was: colony 3a = 12, colony 7a = 1,149, colony 8b = 305, and colony 13a = 575.

Colony characteristics and nesting associates

Colony 7a was located in a permanent 242 ha marsh unit that was dominated by early-successional hardstem bulrush (*Scirpus acutus*): Colony 8b was in a 302 ha permanent marsh characterized by early-successional hardstem bulrush interspersed with cattail (*Typha latifolia*). Colony 13a was located within a 1,334 ha unit with approximately 800 ha of seasonal marsh habitat dominated by early-successional hardstem bulrush. Ibis colonies 7a and 13a shared the following avian associates: Black-crowned Night Heron (*Nycticorax nycticorax*), Snowy Egret (*Egretta thula*), Great Egret (*Casmerodius albus*), Franklin's Gull (*Larus pipixcan*), and Forster's Tern (*Sterna foresteri*). Colony 8b, however, was exclusively associated with Forster's Terns and Franklin's Gulls.

Clutch size and nest initiation date

The mean initiation date for all nests was 24 May (Table 3), but individual colonies averaged from 14 May (colony 7a) to 28 June (colony 3a). Ibis nesting in colony 7a were the first to initiate nests (Table 3). For all colonies combined, clutch size was negatively correlated with nest initiation date ($r = -0.30$, $P = 0.001$).

Apparent nest success and fledgling production

Overall, reproductive success was high, averaging 85% nest success for the incubation period, 82% hatchability, 97% whole and partial brood survival, and 2.06 fledglings per nest (Table 4). Colony 7a had the highest nest success and produced the greatest number of fledglings per nest, whereas colony 13a had the lowest nest success and the fewest fledglings per nest (Table 4).

Nest success (Mayfield method)

Daily survival rates were extremely high (≥ 0.986) and did not vary between colonies during the incubation period ($Z \leq 0.89$, $P \geq .10$) or the nestling period ($Z \leq 1.57$, $P \geq .10$). Overall survival rates did not differ between the incubation ($DSR = 0.991 \pm 0.003$) and nestling periods (DSR =

Table 3. Number of breeding pairs, mean nest initiation date, and average clutch size for all monitored nests of White-faced Ibis within Lower Klamath National Wildlife Refuge (LKNWR), California, 1995.

Colony	Number of breeding pairs[a]	Mean ± SD (range)		Sample size[b]
		Nest initiation date	Clutch size	
3a	12	19 June ± 6 (15-28 June)	2.50 ± 0.58 (2-3)	4
7a	1149	14 May ± 2 (10-20 May)	3.23 ± 0.58 (2-4)	40
8~~a~~b	305	31 May ± 4 (26 May-10 June)	2.93 ± 0.93 (1-5)	41
13a	575	25 May ± 7 (14 May-12 June)	3.30 ± 0.79 (1-5)	45
Overall[c]	2041	24 May ± 10 (10 May-28 June)	3.14 ± 0.79(1-5)	130

[a] Estimated by sunrise flyout counts (colonies 3a, 7a, 8b) and aerial census (colony 13a).
[b] Sample size of monitored nests used for nest initiation date and clutch size analyses.
[c] Overall total for all monitored nests on LKNWR.

Table 4. Apparent method of nest success for all White-faced Ibis colonies on Lower Klamath National Wildlife Refuge (LKNWR), California, 1995.

Colony	% nest success[a] (n[b])	% hatch[c] (n[d])	% whole brood survival (n[b])	% partial brood survival (n[e])	Number of fledglings/nest[f]
3a	25 (4)	100 (3)	100 (1)	100 (3)	0.63
7a	91 (35)	86 (104)	92 (13)	97 (33)	2.26
8~~a~~b	88 (40)	84 (107)	100 (30)	96 (74)	2.08
13a	83 (40)	77 (110)	96 (23)	98 (56)	1.98
Overall[g]	85 (119)	82 (324)	97 (67)	97 (166)	2.06

[a] Percent nest success for the incubation period.
[b] Total number of nests calculations were based on.
[c] Percent hatchability.
[d] Total number of eggs calculations were based on.
[e] Total number of chicks calculations were based on.
[f] Number of fledglings (6-10 days old) produced per nest, calculated as clutch size (See table 2) * nest success * hatchability * whole brood survival * partial brood survival.
[g] Overall total for all monitored nests on LKNWR.

Table 5. Mayfield estimates of nest success for White-faced Ibis during the incubation and nestling periods on Lower Klamath National Wildlife Refuge (LKNWR), California, 1995.

	Incubation Period						Nestling Period						
	Number of			Daily Survival		%	Number of			Daily Survival		%	Overall
Colony	Nests	Days	Losses	Rate	SE[a]	nest success[b]	Nests	Days	Losses	Rate	SE[a]	nest success[c]	nest survival[d]
7a	40	445.5	3	0.993	0.004	84.0	37	171.0	1	0.994	0.006	95.5	80.1
8b	41	349.5	5	0.986	0.006	68.8	36	239.0	0	1.000	0.000	100.0	68.8
13a	45	652.0	5	0.992	0.003	81.8	40	260.5	3	0.989	0.007	91.2	74.6
Total[e]	126	1447.0	13	0.991	0.003	79.1	113	670.5	4	0.994	0.003	95.3	75.4

[a] SE using Johnson 1979.
[b] Nest success for the incubation period calculated as (Daily survival rate for laying + incubation)^{26} * 100; Johnson 1979.
[c] Nest success for nestling period calculated as (Daily survival rate)^{8} * 100; Johnson 1979.
[d] Overall nest survival from start of laying to fledging (i.e. 8 days old) calculated as (% incubation period nest success * % nestling period nest success)/100.
[e] Total for colonies 7a, 8b, and 13a.

0.994 ± 0.003; $Z = -0.71$, $P \geq .10$), although we kept these periods separate for calculating overall nest survival, which averaged 75% (Table 5). Of the 17 nests that failed, 13 were lost during the incubation period: (6 depredated, 7 abandoned) and four were lost during the nestling period (3 depredated, 1 abandoned). Of the eight abandoned nests, one was abandoned with eggs intact, two had cracked and/or flattened eggs in the water near the nest, four had cracked and/or flattened eggs still in the nest, and one had a dead flattened chick still in the nest.

Counts of ibis flying at sunrise to agricultural lands

The percent of breeding ibis (estimated at 4,082 individuals; see above) traversing to agricultural lands at sunrise to forage on private agricultural lands ranged from 21% (853 birds) on 5 June to 84% (3,419 birds) on 18 July ($\bar{x}$ = 52%, SD = 0.26). Between 29 June (count #3) and 4 July (count #4) ibis foraging flights shifted from a northeasterly direction to a northwesterly orientation.

Habitat Use Transects

Of the 10 HUT surveys conducted, 100% of the 29 flocks used alfalfa, ungrazed cattle pastures, and grazed cattle pastures even though only 63% of the total fields on the HUT were comprised of these three field types (Table 6). Mean flock size of birds in these three habitat types was 77 (SD = 107.15, range = 1 - 510) and the average distance of flocks from the nearest road was 376 meters (SD = 486.90, range 20 - 1609). Flock size and distance from the road were not significantly associated ($P = 0.89$, $R^2 = 0.001$). In addition, the grazed cattle pastures on Lower Klamath NWR's northern boundary (i.e. directly north of highway 161) were repeatedly used.

The estimated vegetation height of all sampled fields ranged from 0 to 49 cm ($x = 20.7$, SD = 14.11). The relationship between flock size and vegetation height was not statistically significant ($P = 0.15$, $R^2 = .086$). The estimated number of irrigated fields available on a given HUT ranged from 5 to 17 ($x = 10.1 \pm 4.28$). Of the total number of flocks sampled across the 10 surveys conducted, 97% were in fields with standing water present (of 29 total flocks, 1 was in flooded alfalfa, 2 were in flooded ungrazed pasture and 25 were in flooded grazed pasture).

Foraging Efficiency

Since the majority of birds foraged in pasture or wetland habitats, all foraging efficiency observations were made in these field types. For both habitats combined,

Table 6. Availability and ibis use of seven field types encountered on the habitat utilization transect (HUT) sampled for foraging White-faced Ibis in the Klamath Basin of Oregon, 1995.

Field Type	Number (% of total) of fields on HUT	% of total flocks observed[a]
Alfalfa	75 (25)	3
Fallow	4 (1)	0
Grazed cattle pasture	77 (25)	90
Onion and Sugar beet	22 (7)	0
Potato	34 (11)	0
Small grains	54 (18)	0
Ungrazed cattle pasture	39 (13)	7
Total[b]	305	--

[a] Summed across all 10 HUT's.
[b] Total number of fields on the HUT.

adults were significantly more efficient at foraging than were juveniles (Table 7). Comparisons of foraging efficiency within habitat types revealed that while adults foraged twice as efficient as juveniles in wetlands, adult and juvenile foraging efficiencies were no different in pastures (Table 7).

In both feeding habitats, the probe maneuver was used more extensively than any other foraging maneuver by both juveniles and adults (Table 8). In pastures, most birds probed and the "scissor" method was used almost exclusively in wetlands (Table 8). In wetlands, both age classes were found in foraging water depths less than half the length of the tarsometatarsus, while in pastures, the foraging water depths of both juveniles and adults were more varied, with birds found in all water depth categories (Table 8).

DISCUSSION

Our data indicate a very high reproductive success for ibis on Lower Klamath NWR. Our overall estimates of apparent nest success (85%) were higher than those previously reported for ibis (i.e. $\leq$ 69%; Kotter 1970, Kaneko, 1972, Capen 1977, Alford 1978). Follansbee and Mauser (1994) also reported very high apparent nest success

Table 7. Adult and juvenile foraging efficiency, during the breeding season, on pasture and wetland habitats within the Klamath Basin of Oregon, 1995.

Habitat type (n)	Mean foraging efficiency ± SE		Mean difference in foraging efficiency[a] ± SE	T[a]	P-value[a]
	Juvenile	Adult			
Pasture (148)	0.17 ± 0.02	0.20 ± 0.03	0.03 ± 0.03	1.03	0.1535
Wetland (86)	0.22 ± 0.02	0.44 ± 0.04	0.22 ± 0.05	4.57	0.0001
Combined[b] (234)	0.13 ± 0.02	0.22 ± 0.02	0.09 ± 0.03	3.25	0.0007

[a] T and P values are for the one-tailed alternative that the mean foraging efficiency difference (adult - juvenile) is > zero.
[b] Combined includes pasture and wetland observations.

Table 8. Feeding maneuver(s) and foraging water depths (categories) of sampled juvenile and adult ibis in pasture and wetland habitats during the breeding season within Klamath Basin, Oregon, 1995. Values are the percent of sampled individuals performing each maneuver (for each age class, n = 69 in pasture and n = 38 in wetland) and feeding in each depth category (for each age class, n = 74 in pasture and n = 43 in wetland).

		Foraging maneuver						Water depth		
Age class	Feeding habitat	SC[a]	PR[b]	PE[c]	SC/PR[d]	SC/PE[e]	PR/PE[f]	A[g]	B[h]	C[i]
Juvenile	Pasture	1	84	0	6	0	9	70	18	12
Adult	Pasture	1	88	0	0	0	10	80	12	8
Juvenile	Wetland	8	68	0	24	0	0	100	0	0
Adult	Wetland	11	55	0	29	0	5	100	0	0

[a] "Scissor" maneuver, see text for definition.
[b] Probe maneuver.
[c] Peck maneuver.
[d] Both "scissor" and probe maneuver performed during sampling period.
[e] Both "scissor" and peck maneuver performed during sampling period.
[f] Both probe and peck maneuver performed during sampling period.
[g] Water depth less than half the length of the tarsometatarsus.
[h] Water depth greater than half the length of the tarsometatarsus.
[i] No water present.

(96.6%) for an ibis colony on Lower Klamath NWR during the year previous to our study. Our colony estimates of hatchability, whole brood survival, and partial brood survival were greater than any reported for ibis (Kotter 1970, Kaneko 1972, Alford 1978, Schreur 1987, Henny and Herron 1989). The estimated number of fledglings produced per nest on Lower Klamath in 1995 was higher than Kotter (1970) and Kaneko (1972), but lower than those reported elsewhere (Henny and Herron 1989, Schreur 1987, Follansbee and Mauser 1994). Differences in the above mentioned reproductive parameters across geographic areas are probably the result of annual and site specific variation in climate, habitat conditions, and predator communities. In addition, the methodology used in other studies often differed from ours.

Our Mayfield estimate of nest success for all colonies on Lower Klamath NWR during the incubation period (79%) was slightly lower in comparison to the apparent method (85%). This comparison demonstrates that the Mayfield method is a more conservative estimate of nest success. Other ibis studies have only used the apparent method of nest success, and these estimates are still relatively lower than our Mayfield estimates of nest success for Lower Klamath NWR ibis. The Mayfield method has been recognized as a more robust and reliable estimator of nest success (Johnson 1979, Hensler and Nichols 1981) and therefore, we advocate the use of the Mayfield method for future studies of ibis reproductive success.

Ibis clutches laid later in the breeding season averaged slightly smaller than earlier clutches and are suggestive of the well documented pattern of the seasonal decline of clutch size in birds (Lack 1968). Similarly, in other ibis studies, clutch sizes partially declined with later laying dates (Alford 1978, Steele 1980, Henny and Herron 1989).

All nesting colonies were located in earlier successional hardstem bulrush marshes while all nests were found exclusively in this common nesting substrate for Great Basin ibis (Kaneko 1972, Sharp 1985, Henny and Herron 1989, Hancock et al. 1992, Cornely et al. 1994, Kelchlin 1994). Prior to the 1980's, Lower Klamath NWR consisted of relatively few early-successional emergent marshes because most marsh units were managed as long term permanent wetlands or seasonal wetlands in which the timing of drawdown resulted in plant species more typical of upland sites (Follansbee and Mauser 1994). In the early 1980's, the refuge 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 management practice resulted in the expansion of emergent plants, particularly thin stands of hardstem bulrush in which all ibis breeding colonies on the refuge have been located (Follansbee and Mauser 1994). Although the emergent vegetation in colony 8b was comprised of approximately 60% hardstem bulrush and 40% cattail, only hardstem bulrush was used for nesting. Similar preference for hardstem bulrush have been reported in cases where both cattail and hardstem are present (Alford 1978, Kelchlin 1994).

A large percentage of the ibis population traveled north of Lower Klamath NWR at sunrise to forage on private agricultural lands within the Klamath Basin indicating the importance of private lands to feeding birds. The observed shift during the nesting cycle of foraging flocks flying north of the refuge at sunrise was most likely associated with temporal changes in the availability of favorable (i.e. flooded) foraging habitat on private agricultural lands.

Foraging studies have found that ibis prefer to feed in flooded agricultural habitats (Belknap 1957, Cogswell 1977, Bray and Klebenow 1988). Bray and Klebenow (1988) found that foraging ibis preferred flooded alfalfa fields. Although the number of alfalfa fields and grazed cattle pastures was nearly equal on our HUT, our data indicate that foraging ibis strongly preferred grazed cattle pasture throughout the entire breeding season (Table 6). Some waterbird species have been shown to benefit from grazed pasturelands owing to the increased availability and abundance of prey (Barnard and Thompson 1985, Lo and Fordham 1986, Colwell and Dodd 1995). On various occasions, we observed ibis capturing a favored prey item, earthworms (Bray and Klebenow 1988), which likely became more accessible to foraging birds through pasture irrigation (Grant 1955, Barnard and Thompson 1985, Ryder and Manry 1994). That ibis probed more than any other maneuver in pasture habitat further suggests that they were selecting earthworms. Within the Klamath Basin, we often observed high ibis use of grazed pastures almost immediately following the initiation of field irrigation. Foraging ibis may prefer grazed cattle pasture because they were the field type most frequently flooded during the summer months, and the majority pasturelands were relatively close to colony locations. Irrigated cattle pastures appear to be particularly important foraging habitats for both juveniles and adults late in the breeding season (July-September) when seasonal wetlands on Lower Klamath NWR are being drawn down or are already dry.

Similar juvenile and adult foraging efficiencies in pasturelands may be related to greater availability of potential prey items (e.g. earthworms), thus making foraging relatively easy for inexperienced birds. Juveniles may forage less efficiently than adults in wetlands because prey items are more difficult to obtain, and may require greater skill acquired only through age and experience. For example, we observed juveniles foraging in wetlands trying to eat pieces of dead vegetation and other inedible organic debris, possibly mistaking them for suitable prey items. However, our inferences concerning foraging efficiency in wetlands are potentially limited because samples were taken from only two wetlands.

There have been several hypothesis presented to explain the rapid ibis breeding population increase on Lower Klamath NWR (Follansbee and Mauser 1994). One is that the expansion of the breeding population may be associated with the previously described habitat management changes which created favorable nesting and foraging habitat. Secondly, the great increase in the number of breeding ibises may be attributed to their increased nest success and thus the rising number of recruits into the breeding population in successive years. Finally, the increase may be partially due to ibises displaced from breeding grounds of the Great

Salt Lake marshes which were drastically reduced by flooding from 1982 through 1985 (Ivey et al. 1988). We suspect the high nest success and fledgling rate for ibis on Lower Klamath NWR can be attributed to one or more of the following: 1) sturdy and favorable nesting habitat (hardstem bulrush), 2) accessible foraging habitats within the refuge and adjacent private cattle pastures which contained abundant resources throughout the entire nesting cycle, 3) colonies were flooded during nesting, thus making them relatively inaccessible to mammalian predators, 4) low densities of Franklin's Gulls and other potential avian predators, and 5) a relatively favorable climate during the nesting cycle.

In conclusion, ibis nesting locations have been known to vary considerably between years, where certain sites are used repeatedly while others only intermittently (Ryder 1967). This nomadic nesting pattern is thought to be associated with annual fluctuations in the hydrology of wetlands used as breeding grounds (Ryder 1967). Lower Klamath NWR has a relatively stable water supply and thus, certain refuge wetlands can be managed for early successional emergent marshes of hardstem bulrush, while still meeting traditional habitat management requirements for waterfowl. Therefore, among breeding localities within the Great Basin, Lower Klamath NWR has great potential to become a significant breeding stronghold for ibis populations in the future.

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