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Reproductive success of the Crested Ibis *Nipponia nippon*

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Summary

The last remaining population of the Crested Ibis *Nipponia nippon* in the wild was studied in the Qinling Mountains, Yangxian County, Shaanxi Province, central China, over 24 breeding seasons with particular attention being paid to the nesting behaviour and breeding success. The average clutch size varied significantly among years (2.84 ± 0.77; $n = 271$), suggesting that food abundance, which was distinct in different areas, was indeed a limiting factor. The mean hatching success was 80.2%, and ranged from 35.7% to 100%. Egg losses were due to three reasons: infertility or the eggs being addled, predation, and human disturbance. Three reasons accounting for chick death were highlighted: shortage of food, predation, and disturbance from local inhabitants. However, the overall breeding success of the Crested Ibis, which averaged 65.6%, was much higher than that of many nidicolous birds and was clearly dependent not only on the stability of pair maintenance but also on human conservation and protection measures. The relatively higher proportion of unsuccessful nests at altitudes between 500–700 m and 701–900 m was linked with the more frequent human activities, predation and lower stability of nest-trees in such areas. The fact that there was no significant variation in the number of successful nests or breeding success across different altitudinal zones demonstrated that, to a large degree, habitats used by the Crested Ibis were now suitable for breeding. The rapid increase in the species' numbers in recent years has been achieved through effective protection measures, including legislation, management of population and habitat, and regular surveys and monitoring. A reintroduction programme has been put into effect, protecting the population from a chance catastrophe such as communicable diseases within its limited range.

Introduction

The Crested Ibis *Nipponia nippon* was listed as Critically Endangered by Collar *et al.* (1994) and on the IUCN Red List until 2000. However, its Red List category was changed to Endangered (BirdLife International 2000, 2001, and listed as such on IUCN Red Lists since 2000) because of the increase in the wild population at Yangxian. Overexploitation and destruction of habitat led to the successive extinction of the Russian, Korean and Japanese populations during the twentieth century (Won 1971, Archibald and Lantis 1978, Yamashina and Nakanishi 1983). The reasons for its decline in Russia may have been related to the reclamation of marshlands and illegal hunting (Shulpin 1936). In Japan, the dramatic collapse in its numbers took place during the Meiji Restoration, when traditional conservation measures were disregarded and rampant hunting decimated the population (Yasuda 1983). The small remnant populations that survived there were affected by human disturbance, agricultural changes causing paddies to dry up in winter, and agrochemical use in the 1950s and 1960s, which greatly reduced the availability of the insect prey (Satoh 1978). Illegal hunting was probably the main cause of its decline in the early twentieth century in Korea (Austin 1948). Its decline in central China was probably caused by logging of mature trees, the draining of rice paddies in winter, the widespread use of fertilizers and other agrochemicals, hunting, reduction of food supply, and industrial pollution (Shi *et al.* 1991). The Chinese population, once also thought to be extinct from the 1960s, was rediscovered in Yangxian, Shaanxi Province in 1981 (Liu 1981). Since then great conservation efforts have been made by the Chinese government to restore both the *in situ* and *ex situ* populations. In the past 24 years, the wild population has increased from 7 individuals to approximately 360, with another 422 birds in captivity.

The breeding biology of the Crested Ibis has been documented since its rediscovery (Shi *et al.* 1989, Zhai *et al.* 1994, 2001). A number of factors influencing breeding success were reported by Shi *et al.* (1991) at a time when fewer than 20 individuals inhabited only areas above 1,000 m and where lower-intensity agriculture was still practised prior to 1990. Factors affecting breeding success have now escalated with the rapid growth and dispersal of the ibis population to densely populated areas.

Evidence that food is a limiting factor during the breeding season has been published in a number of studies of altricial birds (Lack 1954, Drent and Draan 1980, Hussell and Quinney 1985, Martin 1987, Dhindsa and David 1989). However, there are other external environmental and intrinsic factors, independent of food abundance, which also affect breeding success. Examples include predation, such as that by skuas that accounts for most of the nesting failures of the Cape Petrel *Daption capense* (Weidinger 1998), together with other aspects of avian predation (Hunter 1991, Emslie *et al.* 1995). Likewise, atrocious weather conditions can have a significant effect, an example being the effect of snow storms on penguins, which is the most important determinant of their breeding success over breeding seasons (Jakubas 2005, Büßer *et al.* 2004). On the other hand, factors such as laying date, divorce rate, even nestling size rank, can also influence breeding success of birds (Thomas *et al.* 1999, Pezzo *et al.* 2001, Dubois and Cezilly 2002).

The aim of the present paper is to examine the variation in the parameters of breeding success of the Crested Ibis in the Qinling Mountains, Shaanxi Province, China, during 24 breeding seasons and to assess the relative importance of each factor.

Study area and methods

The fieldwork was conducted in Yangxian County (33°02′–33°43′ N, 107°11′–108°03′ E; Figure 1), Shaanxi Province, China, on the south slope of the Qinling Mountains during the 24 years from 1981 to 2004. Details of the study area are given by Shi *et al.* (1989, 2001), Li *et al.* (1999) and Ding *et al.* (2002).

The following data were recorded for a total of 271 clutches: (i) location of the nest (including the town or village where the nest was located, and the longitude, latitude and altitude of the nest-site), (ii) date of laying, (iii) clutch size, (iv) egg losses from each nest, (v) number hatching from each clutch, (vi) nestling losses of each clutch, (vii) number of chicks fledging from each brood, and (viii) species, height and diameter at breast height (DBH) of the nest-tree.

All nesting pairs located between 1981 and 2004 ($n = 271$) were included in the study, other than replacement nesting attempts. Observational methods incorporated the construction of an elevated hide or blind adjacent to the study site. This was usually near the nest-site, enabling observation of the breeding pair as they flew

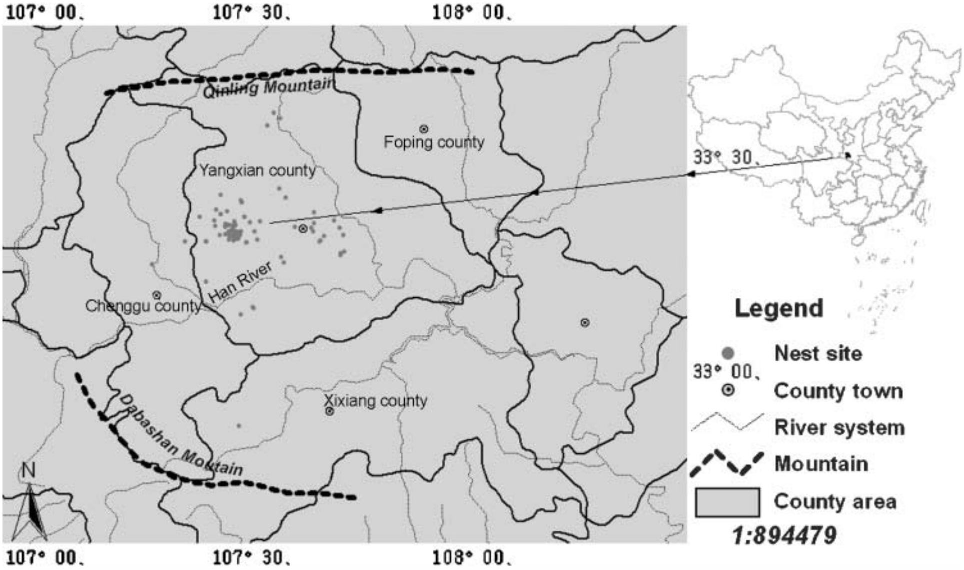

Figure 1. Map of study locations.

around or near the nest from early January to mid-February. Nests were usually at the same site as those of the previous year. The frequent and hoarse calls of the pair, especially the male, aided the location of the birds by observers.

The sex of each of the pair was determined by observations of behaviour during the courtship period. Daily checks were made on nests within the study area to confirm the laying date and the clutch size of all pairs. Annual changes of mean clutch size from 1981 to 2004 were recorded (Table 1). Because of the slight variation in laying dates between different years, different nest-sites and different altitudes, observation periods were varied correspondingly. Eggs were considered to have hatched at 28–31 days and chicks to have fledged at 40–45 days (Shi *et al*. 1989). Causes for egg losses were classified as follows: (i) infertile or addled; (ii) destroyed by nest predators, such as snakes or martens; (iii) other losses, for instance, human disturbance. During the 40-day chick stage, observations of nestling survival were recorded at 3-day intervals.

Since 1987, a total of 326 chicks of about 25 days of age (when their tarsi were in full development but before they were able to move from the nest) have been banded. The rings were provided by the Yamashina Institute of Ornithology and National Bird Banding Centre of China.

Parental care activities of the male and female were recorded for six pairs over four breeding seasons in 1987, 1991, 1992 and 1993, respectively. Data on the activities of both sexes of each study pair were collected over the entire chick stage. These activities included: (i) time spent by the parents feeding the chick; (ii) rate of delivery of food fed to chicks; and (iii) frequency of feeding visits during the chick stage. The daily observations amounted to 2,470 hours in 190 days and were made up of observations from the early morning (06h30) to the late afternoon (19h30) during 40–45 chick stages. A total of 14,008 feeding bouts were recorded.

Altitudes of nest-sites ($n = 231$) were classified into one of three ranges: 500–700 m, 701–900 m, 901–1,100 m. Effects of altitude on clutch size and breeding success were analysed.

Table 1. Clutch size of the Crested Ibis, 1981 to 2004.

Year	Clutch size					Mean	SD	*n*
	1	2	3	4	5			
1981				2		4.00	0	2
1982		1		1		3.00	1.41	2
1983			1	1		3.50	0.71	2
1984			2			3.00	0	2
1985			1[a]	1		3.50	0.71	2
1986	1		2			2.33	1.15	3
1987		1	2	1		3.00	0.82	4
1988		1		2		3.33	1.15	3
1989	1		2			2.33	1.15	3
1990	1		1	1		2.33	1.53	3
1991		1	2			2.67	0.58	3
1992	1		1	2		3.00	1.41	4
1993			5	2	1[b]	3.50	0.76	8
1994		1	3	1	1	3.33	1.03	6
1995		1	4	2		3.14	0.69	7
1996		1	6	1		3.00	0.53	8
1997		2		6	2	3.80	1.03	10
1998		3	6			2.67	0.50	9
1999	1	5	7	4		2.82	0.88	17
2000		3	12	3		3.00	0.59	18
2001	2	16	10	2		2.40	0.72	30
2002		10	19	2		2.74	0.58	31
2003		9	19	6		2.91	0.67	34
2004	1	22	35	2		2.63	0.58	60
	8 (3.0%)	77 (28.4%)	140 (51.7%)	42 (15.5%)	4 (1.4%)	2.84	0.77	271

[a] One of the pairs bred in 1985 and laid 3, 2, 2 and 2 thin-shelled eggs in four consecutive clutches, all failed to hatch. The nest replacement was not recorded.

[b] The first egg was removed and returned to the nest after another 4 eggs had been laid.

Heights and DBH of 230 nest trees (*Quercus variabilis*, $n = 29$; *Pinus massoniana*, $n = 175$; *Ulmus pumila*, $n = 19$; *Pinus tabulaeformis*, $n = 5$; *Populus tomentosa*, $n = 1$; *Platycarya strobilacea*, $n = 1$) were recorded. Effects of *Quercus variabilis* and *Pinus massoniana* on the clutch size and the breeding success were examined.

Results

Laying date and clutch size

A single clutch of 1–5 eggs (usually 3) was laid per year, between 14 March and 8 April. The laying date varied significantly ($t = 13.923$, d.f. $= 50$, $P < 0.001$) between years and averaged 11.2 ± 5.8 ($n = 51$) days after 14 March. The laying date was not significantly delayed with increasing altitude of nest-sites ($r = –0.1$, $P = 0.486$, $n = 51$). In total, 271 clutches (comprising 770 eggs) were laid from 1981 to 2004. The modal clutch size was 3 eggs in most years, except in 1981, 1988, 1992 and 1997 when 4 was the most common clutch size. The percentage of clutches with 1 or 5 eggs was 3.0%, 28.4%, 51.7%, 15.5% and 1.4%, respectively. The average clutch size was 2.84 ± 0.77 ($n = 271$) (Table 1). There was a slight fluctuation in clutch size during the 24 years. From 1981 there was a continuous reduction in clutch size, which reached its lowest level (2.33 eggs) in 1990, followed by a irregular return to 3.8 eggs in 1997, after which there was a fall until 2004 (Table 1). Variations in clutch size during the 24 years were highly significant (t = 32.76, d.f. = 23, $P < 0.001$).

Nesting success

Two hundred and seventy-one clutches were recorded during the 24 years from 1981 to 2004. Among these, the proportion of successful nests, which gave rise to the fledging of at least one chick, was 85.2% (comprising 231 clutches). Accordingly, the proportion of unsuccessful nests which produced no chicks was 14.8% (comprising 40 clutches). The numbers of completely and partially successful clutches were 101 (43.7%) and 130 (56.3%), respectively. Among the latter were 30 clutches with infertile and addled eggs, 4 clutches where the chicks all died before leaving the nest, and 6 clutches that failed to produce any young for both reasons.

Hatching success

The average hatching success was 80.2%, and ranged from 35.7% to 100%, in accordance with fluctuating breeding success during the 24 years (Table 3). There was a marked significant variation in hatching success among years (t = 21.3, d.f. = 23, $P <$ 0.001). As shown in Table 2, hatching success was particularly low in three seasons. These were 1981 (where 50% of eggs hatched), 1983 (where 42.9% hatched) and 1993 (where 35.7% hatched). Egg losses were due to three factors. Infertile or addled eggs, the number of which varied among years (t = 5.4, d.f. = 23, $P < 0.001$), was the most important (a total of 131 eggs in 17 years, as shown in Table 2). Predation was the secondary cause for egg losses, which also varied among years (t = 3.0, d.f. = 23, P = 0.006). A total number of 40 such egg losses were recorded in 9 years. The third cause of egg losses, of less significance than the previous two, was human disturbance, which resulted in a loss of 12 eggs in a 4-year period.

Fledging success

Annual fledging success ranged from 30% to 100% (Table 2). Again this was a factor that differed significantly among years (t = 22.58, d.f. = 23, $P < 0.001$). The overall breeding success of the breeding pairs ranged from 10.7% to 100% (and averaged 65.6%) and varied among years (t = 14.8, d.f. = 23, $P < 0.001$; Table 2). Three reasons accounted for chick death. A shortage of food in the breeding season was the primary cause, resulting in starvation (as shown in Table 3 with a total of 77 nestling mortalities). Secondly, predators such as snakes (especially *Elaphe carinata*), Siberian Weasels (*Mustela sibirica*) and Yellow-throated Martens (*Martes flavigula*) were observed to prey on the Crested Ibis nestlings. Fifteen chicks were lost from nests raided in this way since 1981. The death of a further 10 chicks was considered to be due to disturbance by the local inhabitants that caused the adults to prematurely abandon their nests whilst the nestlings were still nest-bound.

Males and females exhibited almost the same parental roles, both in feeding visits and feeding bouts to chicks throughout a breeding season. Food was delivered to chicks mouth-to-mouth, in the way peculiar to the ibis family, Threskiornithidae. As shown in Table 4, the average frequency of feeding visits per day increased markedly with the brood size (r

Table 2. Variations in breeding success of the Crested Ibis during 24 years (1981–2004).

Year	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992
Nests with eggs	2	2	2	2	2	3	4	3	3	3	3	4
No. of eggs	8	6	7	6	7	7	12	10	7	8	8	12
No. of eggs hatched	4	5	3	6	4	7	9	9	7	8	7	12
No. of infertile eggs	2 (25%)	1 (16.7%)	–	–	3† (42.9%)[a]	–	–	1 (10%)	–	–	1 (12.5%)	–
Predation of eggs	2 (25%)	–	–	–	–	–	3 (25%)	–	–	–	–	–
Other losses of eggs	–	–	4 (57.1%)	–		–	–	–	–	–	–	–
Hatching success	50.0%	83.3%	42.9%	100%	57.1%	100%	75.0%	90.0%	100%	100%	87.5%	100%
Fledging success	75.0%	60.0%	100%	83.3%	100%	100%	55.6%	77.8%	100%	75.0%	71.4%	75.0%
Breeding success	37.5%	50.0%	42.9%	83.3%	30.8%	100%	41.7%	70.0%	100%	75.0%	62.5%	75.0%

Year	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004
Nests with eggs	8	6	7	8	10	9	18	18	29	31	34	61
No. of eggs	28	20	22	24	38	24	48	54	72	85	99	158
No. of eggs hatched	10	16	16	17	30	19	46	47	58	67	69	111
No. of infertile eggs	12† (42.9%)[b]	4 (20%)	4 (18.2%)	4 (16.7%)	7 (18.4%)	5 (20.8%)	2 (4.2%)	7 (13%)	8 (11.1%)	11 (12.9%)	19 (19.2%)	40† (25.3%)
Predation of eggs	3 (10.7%)	–	2 (9.1%)	3 (12.5%)	1 (2.7%)	–	–	–	4 (5.6%)	7 (8.3%)	8 (8.1%)	7 (4.4%)
Other losses of eggs	3 (10.7%)	–	–	–	–	–	–	–	2 (2.7%)	–	3 (3%)	–
Hatching success	35.7%	80.0%	72.7%	70.8%	78.9%	79.2%	95.8%	87.0%	80.6%	78.8%	69.7%	70.3%
Fledging success	30.0%	75.0%	62.5%	82.4%	83.3%	84.2%	78.3%	72.3%	94.8%	100%	98.6%	100%
Breeding success	10.7%	60.0%	45.5%	58.3%	65.8%	66.7%	75.0%	63.0%	76.4%	78.8%	68.7%	70.3%

[a] The cause of the high proportion of infertile eggs in 1985 was that one of the breeding pairs laid 3 thin-shelled eggs in the first clutch.

[b] In 1993, the nest predation that delayed egg-laying of the two breeding pairs contributed to the higher proportion of infertile eggs. The percentage was significantly larger than that of any other year, e.g. 2004, with the exception of 1985 (†$U = 0.679$, $P = 0.497$; $U = 7.01$, $P < 0.001$).

Table 3. Fledging success of the Crested Ibis in 24 breeding seasons, and the number of chicks dead from either starvation or predation or human disturbance.

Year	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992
Nests with chicks	1	2	1	2	1	3	3	3	3	3	3	4
No. chicks fledged	3	3	3	5	4	7	5	7	7	6	5	9
No. chicks died	1	2	–	1	–	–	–	1	–	2	2	3
Died of starvation	1	–	–	1	–	–	–	1	–	2	2	–
Died of predation	–	–	–	–	–	–	–	–	–	–	–	3
Died of disturbance	–	2	–	–	–	–	–	–	–	–	–	–

Year	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004
Nests with chicks	5	5	6	6	10	8	16	17	24	31	34	51
No. chicks fledged	3	12	10	14	25	16	36	34	55	67	68	111
No. chicks died	7	4	6	3	5	3	5	13	3	5	15	20
Died of starvation	2	4	6	2	4	3	4	10	3	5	11	16
Died of predation	2	–	–	1	–	–	1	3	–	–	2	3
Died of disturbance	3	–	–	–	1	–	–	–	–	–	2	1

Table 4. Parental investment by both sexes of the Crested Ibis.

Pair	Brood size	Frequency of feeding visits	Brooding time by males (min)	Difference	Brooding time by females (min)
Pair A	1	4.7 ± 1.4 ($n = 22$)	433.5 ± 88.0 ($n = 22$)	$t = 2.30$ $P = 0.026$	372.3 ± 88.5 ($n = 22$)
Pair B	1	5.1 ± 1.3 ($n = 29$)	368.2 ± 51.3 ($n = 29$)	$t = 2.29$ $P = 0.026$	397.3 ± 45.3 ($n = 29$)
Pair C	2	6.4 ± 2.1 ($n = 27$)	357.6 ± 89.9 ($n = 27$)	NS	336.6 ± 94.4 ($n = 27$)
Pair D	3	7.7 ± 2.7 ($n = 19$)	396.4 ± 82.0 ($n = 19$)	NS	395.4 ± 89.6 ($n = 19$)
Pair E	3	7.3 ± 3.0 ($n = 35$)	349.3 ± 80.6 ($n = 35$)	NS	386.6 ± 81.9 ($n = 35$)
Pair F	4	7.9 ± 2.3 ($n = 27$)	262.0 ± 80.1 ($n = 27$)	$t = 5.83$ $P < 0.0001$	388.1 ± 78.8 ($n = 27$)

$= 0.967$, $P = 0.002$, $n = 6$). Brooding time spent by the male of pair A (433.5 ± 88.0 min, $n = 22$) was significantly higher than that by the female (372.3 ± 88.5 min, $n = 22$) ($t = 2.30$, $P = 0.026$). However, in contrast, the females of pairs B and F spent more time in brooding than the males ($t = 2.29$, $P = 0.026$; $t = 5.83$, $P < 0.0001$). The brooding time spent by pairs C, D, and E was not significantly different between the sexes.

The male parents of each pair did not feed their chicks significantly more often than the female parents except in the case of pair D. Moreover, the amount of food (feeding bouts) provided by parents within a brood of more than one chick decreased significantly with the sequence of hatching, again with the exception of pair D (Table 5). In smaller broods, the first chick received more food than did chicks in larger broods (ANOVA: $F_{4,176} = 10.03$, $P < 0.005$; Table 5).

Effect of altitude on breeding success

The average altitudes of nest-sites of the Crested Ibis, which fluctuated slightly between years, decreased in a highly significant manner over the 24 years ($t = 29.8$,

Table 5. Frequency of feeding bouts delivered to chicks ($n = 13$) by parents of the Crested Ibis[a].

	Pair B	Pair C		Pair D			Pair E			Pair F			
	1st chick	1st chick	2nd chick	1st chick	2nd chick	3rd chick	1st chick	2nd chick	3rd chick[b]	1st chick	2nd chick	3rd chick	4th chick
Feeding bouts by male/day	24.4 ± 9.8 ($n = 40$)	22.7 ± 11.2 ($n = 33$)	18.1 ± 6.8 ($n = 37$)	17.6 ± 10.1 ($n = 37$)	18.4 ± 13.1 ($n = 29$)	16.7 ± 10.3 ($n = 27$)	20.4 ± 10.0 ($n = 29$)	15.2 ± 7.3 ($n = 33$)	6.0 ± 3.6 ($n = 28$)	14.5 ± 6.1 ($n = 42$)	12.3 ± 5.5 ($n = 40$)	12.8 ± 4.7 ($n = 38$)	7.2 ± 4.1 ($n = 18$)
Difference	NS	NS	NS	$t = 2.58$, $P = 0.01$	$t = 2.3$, $P = 0.03$	$t = 2.24$, $P = 0.03$	NS	NS	NS	NS	NS	NS	NS
Feeding bouts by female/day	24.9 ± 12.1 ($n = 40$)	20.3 ± 11.7 ($n = 33$)	15.2 ± 8.0 ($n = 37$)	12.8±5.1 ($n = 37$)	12.3±5.7 ($n =29$)	11.7 ± 5.3 ($n = 27$)	20.0 ± 0.6 ($n = 29$)	15.8 ± 8.5 ($n = 33$)	6.5 ± 4.0 ($n = 28$)	16.4 ± 6.5 ($n = 42$)	14.2 ± 5.9 ($n = 40$)	14.6 ± 6.0 ($n = 38$)	7.9 ± 6.0 ($n = 18$)
Total feeding bouts /day	49.3^c ± 18.2 ($n = 40$)	43.0^c ± 20.3 ($n = 33$)	33.3 ± 11.7 ($n = 37$)	30.4^c ± 11.3 ($n = 37$)	30.7±15.6 ($n = 29$)	28.4 ± 11.1 ($n = 27$)	40.4^c ± 18.6 ($n = 29$)	31.0 ± 14.3 ($n = 33$)	12.5 ± 6.4 ($n = 28$)	30.9^c ± 10.9 ($n = 42$)	26.5 ± 10.1 ($n = 40$)	27.4 ± 8.5 ($n = 38$)	15.1 ± 7.5 ($n = 18$)
Difference		$t = 3.3$, $P = 0.0015$		ANOVA: $F_{2,90} = 0.2$, $P > 0.05$			ANOVA: $F_{2,87} = 29.0$, $P < 0.005$			ANOVA: $F_{2,134} = 17.1$, $P < 0.005$			

1st chick, 2nd chick, etc., refer to the order of hatching.

[a] Feeding bouts of pair A were not recorded.

[b] The 3rd egg was not hatched; the nestling should be the 4th one.

[c] ANOVA: d.f. = 180, $F_{4,176} = 10.0$, $P < 0.005$.

d.f. = 23, $P < 0.001$). However, the average clutch size showed no correlation with the altitude of the nest-sites ($r = 0.19$, $P = 0.37$, $n = 24$). As shown in Table 6, there are differences in clutch size within the three altitude ranges, but these are not significant (ANOVA: $F = 2.42$, d.f. =232, $P > 0.05$). The nesting success was 85%, 84% and 89%, respectively at the three elevations. The number of fledglings per nest and per successful nest, and breeding success, were much the same in the three altitudinal zones (Table 6).

Nest-tree and its effects on breeding success

A total number of 231 nest-trees were recorded during the 24 years, which included *Pinus massoniana* ($n = 175$), *Quercus variabilis* ($n = 30$), *Ulmus pumila* ($n = 19$), *P. tabulaeformis* ($n = 5$), *Populus tomentosa* ($n = 1$) and *Platycarya strobilacea* ($n = 1$). To date the Crested Ibis has bred mainly on the south slope of the Qinling Mountains above 500–1,000 m, where large oaks (*Quercus variabilis*) and pines (*Pinus massoniana*) were available for nesting. Height and DBH differed significantly between the two species ($t = 6.35$, $P < 0.001$; $t = 10.20$, $P < 0.001$, respectively), but the effect of the choice between two main tree species on average clutch size, successful nests, fledglings per nest and per successful nest and breeding success, was not statistically significant (Table 7).

Table 6. Effect of altitude on clutch size and breeding success of the Crested Ibis.

	Altitude range (m)			Difference
	500–700	701–900	901–1100	
Mean clutch size	2.70 ± 0.68 ($n = 106$)	3.00 ± 0.71 ($n = 65$)	2.90 ± 0. 86 ($n = 62$)	$F_{2,230} = 2.42$, $P > 0.05$
Successful nests	93/109 (85%)	57/68 (84%)	51/57 (89%)	NS
Fledglings/nest	1.81 ± 0.99 ($n = 109$)	2.06 ± 1.04 ($n = 65$)	2.00 ± 1.15 ($n = 57$)	$F_{2,218} = 2.32$, $P > 0.05$
Fledglings/successful nest	2.12 ± 0.69 ($n = 93$)	2.35 ± 0.74 ($n = 57$)	2.24 ± 0.97 ($n = 51$)	$F_{2,198} = 1.98$, $P > 0.05$
Breeding success	0.67 ± 0.34 ($n = 113$)	0.68 ± 0.34 ($n = 67$)	0.69 ± 0.33 ($n = 58$)	$F_{2,235} = 1.87$, $P > 0.05$

Table 7. Effect of nest-tree on clutch size and breeding success of the Crested Ibis.

	Species of nest tree		Difference
	Quercus variabilis	*Pinus massoniana*	
Nest-tree height (m)	25.5 ± 3.1 ($n = 29$)	19.7 ± 4.4 ($n = 175$)	$t = 6.35$, $P < 0.001$
DBH (cm)	58.8 ± 32.6 ($n = 29$)	27.1 ± 10.4 ($n = 175$)	$t = 10.20$, $P < 0.001$
Mean clutch size	2.97 ± 0.98 ($n = 29$)	2.79 ± 0.71 ($n = 175$)	NS
Successful nests	27/29 (93%)	149/175 (85%)	NS
Fledglings/nest	2.17 ± 1.16 ($n = 29$)	1.84 ± 1.02 ($n = 175$)	NS
Fledglings/successful nest	2.33 ± 1.04 ($n = 27$)	2.16 ± 0.72 ($n = 149$)	NS
Breeding success	0.70 ± 0.35 ($n = 29$)	0.65 ± 0.34 ($n = 175$)	NS

Discussion

Many species of birds show seasonal, annual, regional, and sometimes local variations in average clutch size. The amount of food provided by the parents is considered the probable dominant factor influencing the evolution of clutch size (Lack 1954). The variation in clutch size among New World passerine birds was related to latitudinal effects, nest predation and nest structure (Kulesza 1989). Latitude clearly is significant only in that it is related to some more relevant ecological variables, such as the amount of available food, which is, in turn, the factor that exerts an effect on the variation of clutch size (Wing 1956). The clutch size of Tree Swallows *Tachycineta bicolor* was significantly larger in years when food was more abundant during the egg-laying period (Hussell and Quinney 1985).

Variations in clutch size of the Crested Ibis between years (Table 1) suggested that food abundance, which varied in different areas, was indeed a limiting factor. The relatively higher clutch size may be related to the plentiful foraging grounds available for the small population (<20 individuals) of the Crested Ibis before 1990 (Ma *et al.* 2000, Shi and Cao 2001). With the rapid growth of the population, new breeders began to occur in lower altitudinal regions and the area of paddyfields used by foraging ibises increased with the corresponding increase in the human population (Ma *et al.* 2000, Ding *et al.* 2000). Selection of nest-sites of the Crested Ibis was positively related to the areas of nearby paddyfields (Li *et al.* 2001). Thus the mean clutch size reached a higher level (3.8 eggs) in 1997 (Table 1). However, after that time the breeding pairs dispersed to lower areas, below 700 m, and the suitability of habitats declined because of a much higher human population and more intensive agriculture (Li *et al.* 1999, 2002). Thus there was a fall in clutch size at that time, as seen in Table 1. We detected no effects of either altitude of nest-sites, or of the characteristics of nest–trees, on the average clutch size (Tables 6, 7).

Effects of supplementary food on reproduction in several species of song sparrows have been reported (Arcese and Smith 1988). Black-billed Magpies *Pica pica* using supplementary food showed an advancement of the initiation of egg laying, higher survival of nest contents (eggs and young) and an increase in fledging success (Manjit and Boag 1990). A total of 18,349 kg of food (mainly loach, *Misgurnus anguillicaudatus*) was supplied to the feeding grounds during breeding seasons over the 24 years (Table 8). The food supplementation was not provided to all breeding pairs, but the weight of supplementary food was significantly correlated with the overall breeding success of each year ($r_s = 0.22$, $P < 0.05$, $n = 24$). Field observations indicated that the foraging success, number of eggs and number of young fledged were indeed markedly higher in years when supplementary food was provided (Lu 1989, Ding 2004).

One of the breeding pairs laid 5 fertile eggs in a clutch successfully in 1993 following removal of the first egg, which demonstrates that egg-laying capacity can be enhanced by artificial means (Cao *et al.* 1995). Other factors may be linked with the fluctuation in clutch size; for instance, one of the pairs laid 3, 2, 2 and 2 eggs with thin shells in four clutches consecutively in 1985, and the pair laid fewer eggs in subsequent years, something that was thought to be due to the previous over-expenditure (Shi *et al.* 1989). Although a detailed study of Western Gulls *Larus occidentalis* by Pyle *et al.* (1991) showed that maternal experience significantly affected clutch size, it is unclear from this study whether or how parental age affects reproductive success of the Crested Ibis.

Table 8. The weight, species and season of supplementary food provided by year[a].

Year	Weight of supplementary food (kg)	Season	No. of food-supplemented nest-sites[b]	Weight of supplementary food/nest[c] (kg)
1981	0			0
1982	320	May	1	320.0
1983	358	April–May	1	358.0
1984	421	April–May	1	421.0
1985	600	May	2	300.0
1986	842	March–May	2	421.0
1987	500	April	3	166.7
1988	1,049	April–May	3	349.7
1989	1,104	April–May	3	368.0
1990	1,120	April	3	373.3
1991	1,043	May	3	347.7
1992	750	April-May	2	375.0
1993	756	April-May	2	378.0
1994	1,105	April	3	552.5
1995	1,187	April–May	3	395.7
1996	457	May	1	457.0
1997	521	April	1	521.0
1998	705	April–May	2	352.5
1999	690	April–May	2	345.0
2000	671	April–May	2	335.5
2001	1,036	April–May	6	172.7
2002	1,232	April–May	5	246.5
2003	1,093	April	5	218.6
2004	789	April	2	394.5
Total	18,349			

[a] The species of supplementary food was mainly loach, *Misgurnus anguillicaudatus*, with a much lower proportion of some coarse fish unidentified in 1996 and 1997.

[b] Not all breeding pairs were provided with supplementary food each year within the breeding season.

[c] The mean weight of supplementary food per nest was significantly correlated with the overall breeding success of each year as seen in Table 2 ($r_s = 0.22$, $P < 0.05$, $n = 24$).

In the Crested Ibis, as mentioned above, the commonest clutch size was 3. It can be seen from Table 9 that 3 was the most efficient clutch size, with hatching success much higher than from clutches of 2 or 4 ($U = 2.84$, $P = 0.004$; $U = 2.03$, $P = 0.042$). The overall survival rate, as seen in Table 9, indicated that the most efficient brood size was likewise 3. It considered that the clutch size of birds has been adapted to correspond with the largest number of chicks for which the parents can, on the average, provide enough food (Lack 1954).

Death of altricial chicks in the early stage, usually 10 days after hatching, is the primary factor affecting breeding success of the Crested Ibis at Yangxian (Shi *et al.* 1991). One hundred and fifty dead individuals were recorded from 1981 to 2003, in which the proportion of nestlings was 60.7% (91 chicks) which were found to have died during chick stage (Ding 2004). In general, nestling death was due to shortage of food, predation, parasites and adverse weather conditions. Firstly, malnutrition of chicks had been noted in some areas linked to the shortage of food (Xi *et al.* 1997). Dissection of birds found dead in the wild showed that 80% had very little food in their stomachs, and the fact that starvation exerts an effect on nestlings directly, could

Table 9. Hatching and fledging success with different clutch sizes.

	Clutch size								
	1	Difference	2	Difference	3	Difference	4	Difference	5
No. of nests	8		80		140		42		4
No. of eggs	8		160		420		168		20
No. of eggs hatched	5		110		336		120		13
Hatching success	62.5%	NS	68.8%	$U = 2.87$, $P = 0.004$	80.0%	$U = 2.25$, $P = 0.024$	71.4%	NS	65.0%
No. of chicks fledged	5		95		301		106		9
Fledging success	100%	NS	86.4%	NS	89.6%	NS	88.3%	NS	69.2%
Breeding success	62.5%	NS	61.7%	$U = 2.84$, $P = 0.004$	70.7%	$U = 2.03$, $P = 0.042$	63.1%	NS	45.0%

be a significant cause of chick mortality (Zhang *et al.* 2000). Secondly, nest predators, such as birds of prey, occasionally attack adult ibises. Significant predators included snakes (especially *Elaphe carinata*), which usually attack eggs and chicks, and weasels, which may also prey on adults as well as their eggs and nestlings (Cao *et al.* 1995, Xi *et al.* 1997, Lu *et al.* 1997, Zhang *et al.* 2000). A total of 40 eggs and 15 chicks were taken by nest predators from 1981 to 2004. Thirdly, parasites have been found to be another cause of mortality, especially in juveniles and adults, in the wild population (12 cases in 1981–2003) (Ding 2004). A total of 17 species of parasitic helminths have been found on both adults and nestlings of the Crested Ibis. The infection rate of chicks was up to 100% and the number of eggs was 1,973–31,510 in 1 g of faeces. Helminthiasises were primarily caused by *Eustrongyloides* sp., *Clinostomum complanatum* and several species of Echinostomadidae (Liu and Yu 2000). However, the heavy infestation by helminths was thought to exert little apparent influence on the nestlings of the Crested Ibis unless the young were also ill due to shortage of food. Finally, climatic factors can exert an important influence on the survival of the Crested Ibis chicks. Spring cold snaps, usually occurring in March and April, also caused losses of chicks during the early chick stage. For example, in May 1993, the nest area in Yangxian County received 86.2 mm rainfall and 149.3 hours of sunlight, with average temperature of 18.2 °C, compared with 30.4 mm rainfall, 210.1 hours of sunlight and mean temperature of 21.3 °C in May 1994 (data from Hanzhong Weather Bureau). It is apparent that the lowest fledging rate of these nestlings (Table 2) may be related to the higher rainfall and lower temperature in May 1993 (Zhai *et al.* 2001).

On the other hand, many species of birds, including the Crested Ibis, start incubating when the first egg has been laid. As a result, the earlier eggs may hatch several days before the later ones. In species of this type the first chicks to hatch have usually already been the sole beneficiaries of the parents' feeding efforts for a time and certainly receive much more food before the younger hatchlings arrive; hence the younger chicks are usually smaller and weaker, and they often die, as shown in Table 10 (Wang and Shi 2000). Thus, 90% of such first hatchings survived. There was a significant reduction ($U = 2.10$, $P = 0.036$) in the survival of second chicks (75%) as the food supply was comparably less than for the first chicks. This pattern was repeated with the third chicks, who again received less food. However, 71% of third chicks

Table 10. Survival of nestlings with sequence of hatching (%) ($n = 169$) (raw data from Wang and Shi 2000).

Brood size[a]	Brood number	Chick number	Sequence of hatching							mean	Survival/ brood[a]
			1st	Difference	2nd	Difference	3rd	Difference	4th		
1	8	8	75 (6/2[b])		–		–		–	75 (6/2)	0.75
2	11	22	81 (9/2)	$U = 2.57$, $P = 0.01$	27 (3/8)		–		–	54.5 (12/10)	1.09
3	29	87	93 (27/2)	NS	89(26/3)	NS	73 (21/8)		–	85 (74/13)	2.55
4	13	52	100 (13/0)	NS	85 (11/2)	NS	69 (9/4)	$U = 1.96$, $P = 0.05$	31 (4/9)	71 (37/15)	2.85
Total/mean	61	169	90 (55/6)	$U = 2.10$, $P = 0.036$	75 (40/13)	NS	71 (30/12)	$U = 2.64$, $P = 0.008$	31 (4/9)	76 (129/40)	

[a] 6/2: The numerator (6) is the number of surviving chicks, and the denominator (2) is the number of dead chicks.

[b] The average number of fledglings per brood was related to the brood size ($r = 0.959$, $P = 0.041$, $n = 4$).

fledged successfully and the reduction in food availability between the second and third chicks was observed to make only a slight difference. The fourth nestlings hatched a week or more later than other siblings and were markedly of smaller size and less able to compete. Only 31% of such chicks successfully fledged (Table 10). Thus the survivability of the Crested Ibis siblings decreases with the sequence of hatching. Lack (1954) suggested that the asynchronous hatching and the consequent difference in the size of the young in the early stages is an adaptation for bringing the brood size into closer adjustment with the food supply. Although siblicide was a main reason of death for up to 88% of the chicks of the Grey Heron *Ardea cinerea* (Stotskaja 1984), and antagonistic behaviours always occurred when the brood size was more than 1 in the Crested Ibis, siblicide itself seems to be of negligible importance. The fact that younger chicks received as much food as older ones on the same day showed that siblings in a brood can be considered as in a stable competitive sequence when food supply is rich (Yu *et al.* 1997). The fact that frequency of feeding visits (and thus the amount of food available to the nestlings) increased with brood size (Table 4) was explained as a behaviour adjustment by the parent birds to get enough food for nestlings.

Trivers (1972) suggested that in most monogamous birds, females show a slightly greater parental investment than males. However, studies of parental care in seabirds display evidence to the contrary. Courtship feeding activities and extensive chick feeding contributions made by male Common Terns *Sterna hirundo* appear to outweigh parental contributions by those of the female (Wiggins *et al.* 1986), and male Black Skimmers *Rynchops niger* provided more parental care than their female partners over the course of a breeding bout (Burger 1981). This seems to be similar to the study on Western Gull *Larus occidentalis* (Pierotti 1981). However, the relative investment by the two sexes of the Crested Ibis was similar in some breeding pairs (Table 4, 5).

Among passerine species with open nests, the proportion of eggs which give rise to flying young is somewhat under half, with an average of about 45% (Lack 1954). The overall breeding success of the Crested Ibis presented in Table 2 is thus much higher than that of many birds recorded by Royle *et al.* (1999). At the individual level, divorce is currently regarded as an adaptive strategy by which individuals improve their mating status, and hence their success (Diamond 1987). This has often been construed to imply that pairs with low breeding success should be more likely to divorce than those that breed successfully (Coulson 1966, Ens *et al.* 1996). The results of meta-analysis indicate that there is indeed an overall significant pattern of higher divorce rates in failed pairs compared with successful ones (Dubois and Cezilly 2002). It is characteristic of breeding pairs of Crested Ibis that the pair bond will be kept for many years, once formed (Lu *et al.* 1997). Thus the relatively higher breeding success of the Crested Ibis should be linked to the stability of pair retention. Furthermore, this was also thought to be related to human conservation efforts. Given the rapid increase and wider distribution of the population, the intensity of human protection will be reduced correspondingly. If so, lack of field evidence means we do not know whether the birds in newly colonized areas have significantly lower reproductive success.

The Crested Ibis once occurred in plains near human settlements which have abundant large trees for nesting and suitable wetlands for feeding (Swinhoe 1873, La Touche 1934). But overexploitation and destruction of habitat led the Russian, Korea and Japanese population to successive extinction during the twentieth century

(Yamashina 1967, Archibald *et al.* 1980) and the population in China declined to near extinction. For the same reason, the wild population in Yangxian survived only in more mountainous districts with the lowest human populations (Shi *et al.* 1989, Shi and Cao 2001). With the improvement in the environment, the species has more recently shown a preference to move back to lower land for breeding (Ma *et al.* 2000, Ding *et al.* 2000).

The data presented here confirm that some nest-sites are more suitable than others. As seen in Table 6, the relatively higher proportion of unsuccessful nests in regions where the altitude is between 500–700 m and 701–900 m was linked with the more frequent human activities, predation and lower stability of nest-trees in such areas (Cao *et al.* 1995, Shi and Cao 2001). The fact that there was no significant variation in the number of successful nests and the breeding success between different altitudinal regions (Table 6) demonstrated that, to a large degree, habitats used by the Crested Ibises were now suitable for breeding, consistent with results of selection for nest-sites (Li *et al.* 2001).

Table 7 shows that *Quercus variabilis*, which is much higher and stronger than *Pinus massoniana*, was much more inaccessible to predators and thus breeding pairs show a preference for it as a nest-tree (Li *et al.* 2001). Breeding pairs nesting on *Quercus variabilis* displayed a slight increase in clutch size, number of successful nests, fledglings per nest and breeding success compared with those opting for *Pinus massoniana*. However, with the decrease in elevation of nest-sites, Crested Ibises were forced to choose *Pinus massoniana* for nest-trees, as this is the dominant arboreal component in the local flora below 900 m of altitude in these areas (Shi and Cao 2001, Ding 2004).

This distinctive species has now become extinct over most of its former range and is limited to a single area in Yangxian, where it has a relatively small population. The rapid increase in Crested Ibis numbers in recent years, particularly since 1999, has been achieved through effective protection and management of its nesting and feeding habitats. We should place emphasis on the protection measures that have been taken, as follows.

The Crested Ibis is listed as a National Protected Species (Category I) in China. The government of Yangxian County immediately announced emergency regulations to prohibit logging, the use of agrochemicals in paddyfields and the use of the firearms for hunting when the nesting birds were discovered in May 1981. To date, 150 large nesting trees have also been declared state property (Ding 2004).

As accidental killing of this species sometimes occurs (Zhang *et al.* 2000), a national nature reserve was established in 2004 within areas the species inhabits, especially nesting areas. The nest-trees are patrolled and protected during the breeding season until the chicks successfully fledge (Shi and Cao 2001). The trunks of the nest-trees, as well those of as adjacent trees, are covered with plastic cloth or sharp blades to prevent snakes climbing up them (Cao *et al.* 1995) and nylon nets are placed under the nests to catch chicks falling out (Shi and Cao 2001, Ding 2004). As mentioned above, extra food was provided to the birds, especially in the breeding season, and the ice in paddies was broken on cold days to maintain feeding areas (Lu 1989, Zhang *et al.* 2000). Moreover, banding of nestlings, radio-tracking and environmental pollution monitoring are very helpful for management of the population (Shi and Cao 2001, Ding 2004). With the dispersal of the population, many nearby counties and cities have been visited by individuals looking for new nesting and wintering sites, and it is very difficult to take the same measures in areas with a larger human population. Thus the establishment of a model of community management plays an important part in encouraging the local habitants to participate in conservation of the Crested Ibis (Ding 2004).

However, we are still faced with a host of difficulties in the management of the endangered population and its habitat. For example, the wetlands along Hanjiang River have become an important foraging ground for the Crested Ibis in recent years, so supplementary food should be provided to the wild birds there outside breeding season, and more public education and promotion is required (Xi *et al*. 1997, Zhang *et al*. 2000).

It has been suggested that the present population of the Crested Ibis in Shaanxi should gradually be dispersed to other parts of its former range in China, as the wild population is currently vulnerable to extinction through a chance catastrophe within its limited range (Fan 2000). Because part of the former habitat of the Crested Ibis in Russia is in a comparatively good condition, a reintroduction programme could be considered there in the future (Litvinenko 2000). When the captive population in Japan has increased sufficiently, with the help of the Chinese government, a reintroduction programme at carefully selected sites could also be considered (Toshio 2000). As preparation for reintroduction, preliminary surveys in Shaanxi, Gansu, Henan and Zhejiang Province, where the Crested Ibis lived in the past, have been conducted during winter 2003. In October 2004, 12 captive-bred individuals were released at Huayang Town (33°34.112 N, 107°30.865 E) in Yangxian County where two wild pairs nested for 2 years. Observations show that 12 birds, 5 of them radio-collared, were surviving in good condition (Liu *et al*. 2005).

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