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Cranes of the World: 5. Comparative Reproductive Biology

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5 Comparative Reproductive Biology

The reproductive biologies of cranes are surprisingly similar. All crane species are strictly monogamous, have long pair bonds and a prolonged period of juvenile dependency, and are highly territorial during the breeding season. All cranes also have an extremely limited reproductive potential, resulting from their deferred sexual maturity, low clutch size, and limited renesting tendencies following the loss of a clutch or hatched young.

Yet, within these specific characteristics, there is also a fair amount of species diversity, which is largely associated with adaptation to ecologically diverse breeding habitats and geographic distributions. The most obvious of these adaptations are perhaps the interspecific variations in length of the breeding season and its seasonal timing. This may be readily seen when the monthly distribution of egg records for various species and subspecies of cranes are compared (table 14). Among all the temperate-to-arctic-breeding Northern Hemisphere cranes the egg-laying period is timed to coincide with spring, so that hatching occurs in late spring or early summer. This allows for a maximum length of time for the young to grow and fledge before the first fall storms or snowfalls, and for the young to hatch at near the peak of the early summer emergence of insects and other invertebrate life that they forage on. Even within the sandhill cranes, not only is it apparent that more southerly forms, such as the Florida and Mississippi races, have earlier egg-laying periods, but also the total period during which eggs may be found is greatly prolonged. This period includes a maximum spread of about half a year in the case of the Florida race, and such a wide spread suggests that renesting abilities may be fairly well developed in this race. For example, 20 percent of the egg records occur in three months following the peak month (March) in the Florida race, and 41 percent occur in the two months following the same month in the Mississippi form, while in the Canadian and Alaskan populations only 2 percent of the egg records occur following the peak month (June).

Somewhat similar trends may be seen in the other northern cranes, with all of the species having peaks in the egg records occurring in April (Japanese crane), May (demoiselle, Eurasian, white-naped, and whooping cranes), or June (black-necked crane). Only the Eurasian crane exhibits a range of egg records suggestive of possible renesting significance.

On the other hand, the wattled crane of Africa exhibits an egg-record pattern that covers the entire twelve-month period, although apparently peaking between May and August. Walkinshaw (1964) states that in South Africa the wattled crane is a dry-season (winter) nester, while elsewhere it is said to nest in the rainy season (Konrad, 1981). Only slightly less extended than the wattled crane records are the records for the similarly tropical sarus crane, with records extending from June to March but peaking between July and September, typically shortly after the summer monsoon period. The Australian crane primarily breeds between September and March, with an apparent nesting peak in February. In that general area, the first storms of the wet season occur in October or November, and the wet season typically ends in March or April.

The West African crowned cranes exhibit a remarkably abbreviated breeding season, which is centered in July. In East Africa, this species breeds during the rainy period in most areas, but in the wettest parts of East Africa the dry season is apparently preferred (Brown and Britton, 1980). Similarly, the northern population of the South African crowned crane nests only during the rainy season (April to July) in Zambia, in contrast to the less restricted nesting of the wattled crane (Benson et al., 1971). Farther south the season seems to be concentrated between December and March, which also points to rainy-season nesting. A similar seasonal pattern for nesting occurs in the blue crane, which exhibits a peak

TABLE 14

Percentage Monthly Distribution of Egg Records, Various Cranes*

	Dec.	*Jan.*	*Feb.*	*Mar.*	*Apr.*	*May*	*June*	*July*	*Aug.*
Sandhill crane									
Florida (108)	2	5	24	50	16	3	1	—	—
Mississippi (34)	—	—	3	56	32	9	—	—	—
Michigan (203)	—	—	—	—	62	36	1	1	—
Western U.S. (126)	—	—	—	—	40	55	4	1	—
Canada (43)	—	—	—	—	2	56	40	2	—
Alaska (70)	—	—	—	—	—	6	91	1	1

	Mar.	*Apr.*	*May*	*June*	*July*	*Aug.*
Other northern cranes						
Japanese crane (19)	5	63	32	—	—	—
Demoiselle crane (33)	—	9	78	9	3	—
Eurasian crane (69)	—	29	54	17	—	—
White-naped crane (9)	—	22	56	22	—	—
Whooping crane (Canada, est. 78)	—	—	65	33	—	1
Black-necked crane (10)	—	—	20	70	10	—

	May	*June*	*July*	*Aug.*	*Sept.*	*Oct.*	*Nov.*	*Dec.*	*Jan.*	*Feb.*	*Mar.*	*Apr.*
Tropical & southern cranes												
Sarus crane (63)	—	3	27	22	19	3	3	8	2	8	5	—
Wattled Crane (91)	18	19	13	14	3	9	3	7	4	3	2	4
W. African crowned (15)	—	—	27	67	7	—	—	—	—	—	—	—
Australian crane (27)	—	4	—	—	11	7	4	7	19	41	7	—
Blue crane (61)	—	—	—	—	—	17	26	39	11	6	2	—
S. African crowned (59)	—	—	—	—	—	7	2	22	35	20	12	2

*Data from *Cranes*, vol. 1, no. 1, 1973; sample size in parentheses.

in egg records during the summer months of November and December. In this species' nesting areas about 80 percent of the annual rainfall occurs during the summer months (Walkinshaw, 1973).

It seems to be a fundamental characteristic of all cranes that they are highly dispersed and territorial during the breeding season. Because of these extremely large territories, territorial limits tend to become diffuse, and accurate estimates of territory sizes are thus very difficult to obtain. It is perhaps more realistic to measure breeding densities rather than to estimate territorial sizes, but a sampling of both kinds of approaches is presented in table 15. It may be seen that under rare conditions territories may be as small as 1.2 hectares (about 3 acres), but the average in sandhill cranes is closer to 25 hectares, or well above 50 acres. Similarly, total nesting densities are generally no more than at least 10 square kilometers per pair. The remarkably high sandhill crane breeding densities and small average territorial sizes observed by Drewien (1973) at Gray's Lake, Idaho, were attributed by him to a variety of local factors, including isolation, freedom from disturbance, and abundant breeding habitat.

Within the genera *Grus*, *Bugeranus*, and *Anthropoides*, the clutch size of all species is fairly close to 2.0 eggs. Only very rarely are three eggs present in the nests of these species, and the relatively few records of single-egg clutches are mostly associated with the wattled crane, in which single-egg clutches are common. Thus, for all practical purposes it is fair to say that all cranes except the wattled and crowned cranes consistently lay two-egg clutches (table 16). The crowned cranes exhibit an interesting divergence from this strict pattern and approach three-egg clutches in most portions of their range. Perhaps the only exception is in East Africa, where the data suggest that a slightly smaller average clutch size might be typical there. However, Pomeroy (1980b) has suggested that in this area the clutch size is altitude-dependent, with highland populations having larger clutches than those of lowlands.

It is typical for the size of the eggs of birds to be inversely related to the adult size of the birds; smaller species tend to lay eggs relatively larger than those of larger relatives. Thus, it is not surprising that the largest egg laid by any crane is produced by the smallest species, the demoiselle crane (table 17). Similarly, the eggs laid by the very large species, such as the whooping crane, the Australian crane, and the sarus crane, are among the relatively smallest of all crane eggs. Among the sixteen forms tabulated in table 17, an average weight reduction of 40.6 percent occurs between the

TABLE 15

Breeding Densities and Territory Sizes, Various Crane Populations

Species	*Territory Area (Hectares)*	*Breeding Density Nests or Pairs/km²*	*Reference*
West African Crowned Crane	86-388	—	Walkinshaw, 1973
Demoiselle Crane	—	0.10	Grummt, 1961
Wattled Crane	over 100	under 0.05	Konrad, 1981
Siberian Crane	—	0.001-0.002	Flint and Kistchinski, 1981
Sandhill Crane			
Lesser (Canada)	—	under 0.8	Lewis, 1977
		0.06	Walkinshaw, 1981a
Lesser (Alaska)	—	0.91-1.3	Boise, 1976
Greater (Oregon)	Ave. of 8, 25 (1.2-68.0)	—	Littlefield and Ryder, 1968
Greater (Idaho)	Ave. of 10, 17 (10-23)	ca. 0.25	Drewien, 1973
Greater (Michigan)	Ave. of 89, 57.7 (3-194)	—	Walkinshaw, 1965b
Greater (Wisconsin)	Ave. of 17, 126 (63-168)	max. 0.07	Crete and Grewe, 1982
Florida (Kissimmee)	—	ca. 0.07-0.08	Walkinshaw, 1976
Whooping Crane	Ave. of 18, 720 (40-4, 710)	—	Kuyt, 1981a
Japanese Crane			
USSR	400-1,230	—	Viniter, 1981
China	—	ca. 0.34-0.36*	Ma and Xu, 1980
Japan	—	ca. 0.39*	Masatomi, 1981b
Hooded Crane (Lower Amur)	—	0.019-0.038	Neufeldt, 1981a
Black-necked Crane	45	0.38*	Cheng, 1981
Eurasian Crane			
Germany	—	0.001-0.005	Glutz, 1973
Norway	—	0.015-0.020	Glutz, 1973
Finland	—	0.001-0.018	Merikallio, 1958
Sweden	—	0.015-0.017	Nilsson, 1982

*Estimated (50 percent of reported cranes/km² during breeding season).

fresh-egg stage and the weight of the newly hatched chick, with a range of 34 to 47 percent. There seem to be no significant interspecific differences apparent in this statistic.

There are no obviously significant differences in incubation periods among the species of cranes (table 18). One would expect that the high-latitude cranes should exhibit the shortest incubation periods, and it seems to be true that such forms as the Siberian crane, the Canadian sandhill crane, and the Eurasian crane all exhibit relatively short incubation periods. However, the demoiselle crane, a desert-breeding type, has a surprisingly abbreviated breeding season, to judge from table 14. What does show a rather remarkable interspecific variation is the length of the fledging period. The shortest fledging periods, not surprisingly, seem to be associated with high-latitude nesting, as in such species as the lesser sandhill crane and the Eurasian crane. Yet, the demoiselle has what seems to be the shortest of all crane fledging periods, although this may in part be attributable to its unusually small adult size. Likewise, the crowned crane seems to have a remarkably short fledging period, based on avicultural data, although Walkinshaw (1964) reported the fledging period of the South African form under wild conditions to be about three months. As might be expected, the longest fledging periods are those of the tropical forms, including the sarus crane and the wattled crane, and probably also the Australian crane. Rather remarkably, the blue crane seems to have an extremely variable but protracted fledging period, in spite of its essentially temperate distribution. No obvious explanation for this anomaly is apparent, although van Ee (1966) noted that initial flying by the young

TABLE 16

Clutch-size Variations in Various Crane Populations

Species	Nests	Total Number of Nests of Each Clutch-size: 1	2	3	4	Total Eggs	Average Clutch	Reference
East African Crowned	41	—	—	—	—	—	2.56	Pomeroy, 1980b
West African Crowned	17	0	3	14	0	48	2.47	Walkinshaw, 1973
South African Crowned								
Zambia & Rhodesia	17	4	3	10	0	40	2.35	Walkinshaw, 1973
South Africa	34	3	10	16	5	91	2.67	Walkinshaw, 1973
Blue Crane	61	7	53	1	0	116	1.90	Walkinshaw, 1973
Wattled Crane	90	35	55	0	0	145	1.61	Walkinshaw, 1973
Siberian Crane	12	—	—	—	—	—	1.75	Flint and Sorokin, 1981
Australian Crane	27	6	20	1	0	49	1.82	Walkinshaw, 1973
Sarus Crane	132	4	126	2	0	262	1.985	Walkinshaw, 1973
Lesser Sandhill								
Alaska	71	—	—	—	—	—	1.76	Boise, 1976
Alaska	77	9	68	0	0	154	1.88	Walkinshaw, 1973
Canadian Sandhill								
Canada	53	5	48	0	0	101	1.94	Walkinshaw, 1973
Greater Sandhill								
Oregon	108	9	99	0	0	207	1.92	Littlefield and Ryder, 1968
Michigan	183	8	174	1	0	359	1.96	Walkinshaw, 1973
Idaho	337	24	310	3	0	653	1.94	Drewien, 1973;
Florida Sandhill								
Georgia	6	1	5	0	0	11	1.83	Walkinshaw, 1973
Kissimmee	67	5	62	0	0	129	1.92	Walkinshaw, 1973
Central Florida	121	7	114	0	0	235	1.94	Walkinshaw, 1982
Cuban Sandhill	10	0	10	0	0	20	2.0	Walkinshaw, 1973
Mississippi Sandhill	79	—	—	—	—	—	1.86	Valentine, 1982
Whooping Crane	203	16	184	9	0	393	1.94	Kuyt, 1981b
Japanese Crane	22	1	21	0	0	43	1.95	Walkinshaw, 1973
Eurasian Crane	52	—	—	—	—	—	1.83	Masatomi, 1980
Schleswig-Holstein	17	1	15	1	0	34	2.0	Glutz, 1973
Finland	19	2	17	0	0	36	1.89	Glutz, 1973

might occur earlier if the parents have by then completed their wing molts and again are able to fly. Yet, this does not seem to provide an adequate explanation for the seemingly deferred fledging of this species.

It is to be expected that nesting and fledging success rates (table 19) might be highly variable among species and from year to year in the same species, for these are largely dependent upon local and highly variable factors, such as weather conditions and degrees of local disturbance or predation. However, it would appear that in many cases the nesting success of wild crane populations is rather surprisingly high, occasionally with as many as 70 to 80 percent of the nests that are initiated being successfully terminated. This remarkably high rate of nesting success is probably associated with effective nest defense by the combined efforts of the two adults, which are large enough to deter all but the most persistent predators. The percentage of eggs hatched is similar to that of the percent of nests successfully terminated, suggesting a very low number of eggs that fail to hatch as a result of infertility, dead embryos, or other factors that might reduce hatchability. The rate of fledging success, however, is highly variable and is a difficult statistic to obtain with any degree of certainty. The figures in table 19 suggest that anywhere from about 44 to 71 percent of the eggs laid may result in successfully fledged young under natural conditions. It is a general rule of thumb among crane biologists that no more than one of the two crane young that normally hatch from a clutch will be fledged successfully, owing to intersibling strife. This is clearly not an invariable rule, as the data of Walkinshaw (1976) indicate. Interestingly, the fledging success data for wild whooping cranes for the period 1967-1978 include the time during which single eggs have been removed from whooping crane nests, so that many clutches actually consisted of only a single egg to begin with. The limited data suggest that fledging success of the remaining offspring has increased somewhat during this period, although not so much as one would have predicted if this were a

TABLE 17

Egg, Hatchling, and Adult Weights, Various Cranes

Species	*Estimated Egg Weight (grams)*	*Percent Adult Weight*	*Average Chick Weight (1 day)*	*Percent Adult Weight*	*Estimated Adult Female Weight (kg)*
Crowned Crane	156	4.3	91.7*	2.5	3.6
Blue Crane	181	4.9	120.1†	3.7	3.2
Demoiselle Crane	134	5.7	73.4*	3.1	2.35
Siberian Crane	202	3.8	121.7*	2.3	5.3
Sarus Crane	238	3.5	134.2*	2.0	6.8
Australian Crane	185	3.2	102.3†	1.8	5.7
White-naped Crane	207	4.1	116.3*	2.3	5.0
Sandhill Crane					
Lesser	164	4.8	104.0*	3.1	3.35
Canadian	178	4.7	107.7†	2.8	4.3
Florida	180	4.8	116.4*	3.1	3.75
Greater	204	4.7	119.2*	2.8	4.3
Whooping Crane	212	3.3	124.4‡	1.9	6.4
Japanese Crane	235	3.6	132.0*	2.0	6.5
Hooded Crane	175	5.0	113.7*	3.2	3.5
Eurasian Crane	189	3.7	121.1*	2.3	5.15
Black-necked Crane	222	3.7	118.1**	1.9	6.0

*Archibald and Viess (1979)
†Walkinshaw (1973)
‡Erickson and Derrickson (1981)
**Lu, Yao, and Liao (1980)

TABLE 18

Incubation and Fledging Periods, Various Cranes

Species	*Incubation Period (in days)**	*Fledging Period (in days)*	*Reference (Fledging Period)*
Crowned Crane	28-31	63	Archibald and Viess, 1979
Blue Crane	28-35	at least 110	van Ee, 1966
Demoiselle Crane	27-30	55-65	Cramp and Simmons, 1980
Wattled Crane	35-40	about 150	Konrad, 1981
Siberian Crane	29	76	Michael Putnam (pers. comm.)
Sarus Crane	31-36	120	Rothschild, 1930
Australian Crane	35-36	about 98	Lavery and Blackman, 1969
White-naped Crane	28-32	at least 70	Archibald and Viess, 1979
Sandhill Crane			
Lesser	—	over 60	Boise, 1976
Canadian	27	—	—
Greater	31-32	67-75	Drewien, 1973
Florida	31-32	at least 70	Archibald and Viess, 1979
Whooping Crane	30-35	80-90	Kuyt, 1981b
Hooded Crane	—	75	Michael Putnam (pers. comm.)
Japanese Crane	30-34	about 95	Bartlett, 1861
Black-necked Crane	31-33	about 90	Lu, Yao and Liao, 1980
Eurasian Crane	28-31	63-70	Heinroth and Heinroth, 1926-28

*After Archibald (1974), except for the Siberian crane, which is from Michael Putnam (pers. comm.).

TABLE 19

Nesting and Fledging Success Rates in Various Crane Populations

Species	*Total Nests*	*Total Eggs*	*Nests Successful*	*Eggs Hatched*	*Young Fledged**	*Reference*
Blue Crane	17	34	11(64.7%)	25(73.5%)	—	Walkinshaw, 1963
Lesser Sandhill						
Alaska	6	11	4(66.6%)	7(63.6%)	—	Boise, 1976
Greater Sandhill						
Various states	—	63	—	42(66.7%)	—	Walkinshaw, 1949
Michigan	133	252	(102)77%	(184)73%		Hoffman, 1979
Michigan (Lower)	204	380	161(78.9%)	294(77.4%)	284(96.6%)	Walkinshaw, 1981a
Idaho	326	—	255(78%)	—	—	Drewien, 1973
Oregon	456	—	201(44%)	—	—	Littlefield, 1976
Florida Sandhill						
Loxahatchee	25	44	22(88%)	31(70%)	—	Thompson, 1970
Central Florida	119	224	92(77.3%)	176(77.6%)	174(98.9%)	Walkinshaw, 1982
Whooping Crane						
N.W. Territories (1954-1965)	37	72	30(81.1%)	40(55.5%)	32(80%)	Novakowski, 1966
N.W. Territories (1966-1980)	211	260†	—	156(60%)†	96(61.5%)	Kuyt, 1981a
Eurasian Crane						
Schleswig-Holstein	22(1st)	—	17(77.3%)	—	—	Glutz, 1973
	4(2nd)	—	2(50%)	—	—	Glutz, 1973
	17	34	—	25(73.5%)	—	Glutz, 1973
	41	—	26(63.4%)	—	—	Glutz, 1973
Japanese Crane	—	63	74.4%	(50)79.4%	(22)44%	Masatoma, 1981b

*Fledging success calculated on basis of total eggs that hatched. †Minimum number, excluding eggs removed from the nest.

TABLE 20

Results of Cross-fostering of Whooping Cranes, 1975-1980*

	1975	*1976*	*1977*	*1978*	*1979*	*1980*	*Totals*
Eggs Incubated							
From Canada	14	15	16	13	19	12	89
From Patuxent	0	2	14	15	5	2	38
Total Eggs Incubated	14	17	30	28	24	14	127
Chicks Hatched							
From Canada	9	11	15	9	12	10	66
From Patuxent	—	0	5	5	4	2	16
Total Chicks Hatched	9	11	20	14	16	12	82
Total Egg Losses	5	6	10	14	10	2	47
Hatching Success (%)†	64	65	67	50	67	86	65
Young Fledged							
From Canada	5	4	4	3	6	4	26
From Patuxent	—	0	0	0	2	1	3
Total Young Fledged	5	4	4	3	8	5	29
Fledging Success (%)‡	55	36	20	21	50	42	35
Cranes Reaching Wintering Areas							
Young-of-year	4	3	2	3	7	4	23
Older Age-Classes	—	3	6	6	8	14	37
Total	4	6	8	9	15	18	60
Annual Post-juvenile Mortality	—	1	0	2	1	1	5
Annual Mortality (%)	—	25	0	25	11	6	11.9

*Data for 1975-1977 from Drewien and Bizeau (1978); more recent data from Derrickson (1980) and Drewien (1978-1981). Slightly different figures are provided by Erickson and Derrickson (1981). †Percentage of total eggs incubated. ‡Percentage of total chicks hatched.

critically important aspect of survival in young cranes.

Some of the best data on hatching and fledging success in wild cranes are now available as a result of the cross-fostering experiments involving the placing of whooping crane eggs in the nests of the greater sandhill crane (Drewien and Bizeau, 1978). These eggs have come from two very different sources: from wild whooping cranes in Wood Buffalo National Park, Canada, and from a small captive flock of whooping cranes at Patuxent Wildlife Research Center, Laurel, Maryland. As shown in table 20, hatching success and fledging success of offspring from wild-population eggs are similar to data for wild whooping cranes and other wild crane populations, at least during the first five years of this study. The eggs taken from the wild population exhibited a surprisingly high, 74 percent, hatchability. However, the fledging success of these young was only 29 percent, or appreciably less than available data for young from the wild population. Eggs from the Patuxent population exhibited a 42 percent hatchability and a fledging success of only 7.9 percent, suggesting some serious inherent problems in the viability of eggs and young from this captive stock. Mortality rates of birds following fledging seem to be relatively low, and are probably not significantly different from those of other wild whooping cranes, to judge from the still limited available data.