THE BROOD SIZE OF CRANES

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IN spite of recent studies of populations of North American cranes, relatively little is known about the breeding biology of the species, especially birds that nest in arctic and sub-arctic regions, and their management has been shown to be based largely on assumptions for which there are few supporting data (Miller et al., 1972). We know, for example, that Whooping Cranes (*Grus americana*) and Sandhill Cranes (*G. canadensis*) normally lay two eggs but seldom raise more than one young (Walkinshaw, 1949; Novakowski, 1966), but we do not know whether this is due to extrinsic factors, such as weather, food, or predation that affect the survival of young, or whether it is due to behavioral events that limit the number of young, regardless of proximate ecological factors. This question has important implications for the protection and management of these species, and is also of biological interest.

OBSERVATIONS

Table 1 shows the clutch sizes of 341 nests from breeding populations of two races of Sandhill Cranes, the Florida Sandhill Crane (*G. c. pratensis*) nesting in Florida and Mississippi, and the Greater Sandhill Crane (*G. c. tabida*) nesting in Oregon and Michigan. Clutches of one and three eggs are uncommon and most clutches contain two eggs. The mean for this sample was 1.9 eggs per clutch.

Walkinshaw (1949) estimated that 27 pairs of Greater Sandhill Cranes in Michigan laid a total of 54 eggs, but were observed to raise only 18 full-grown young, or an average of 0.7 per breeding pair. In another study (Walkinshaw, 1965*a*) observed that a total of 45 pairs raised an average of 0.8 young per year per pair between 1952 and 1958. For no apparent reason, the productivity of this population declined to 0.5 and 0.3 young per pair in 1963 and 1964 respectively (Walkinshaw, 1965*b*). A population of Greater Sandhill Cranes at the Malheur Wildlife refuge in Oregon included 160 pairs of breeding adults that produced between 35 and 45 young, or approximately 0.2 to 0.3 young per pair (Littlefield and Ryder, 1966). The low productivity of Sandhill Cranes is partly due to unsuccessful nesting of breeding pairs, but another important factor seems to be that successful pairs seldom raise more than one young.

Family groups that contain more than one young occur in Japanese Cranes (*G. japonensis*) according to Masatomi (1972), and in populations of Greater Sandhill Cranes in Michigan (Walkinshaw, 1965*a*) and Oregon (Littlefield

TABLE 1
THE CLUTCH SIZE OF SANDHILL CRANES

Locality	Number of Nests	Number of Eggs in Nest			Total eggs	Mean Clutch Size	Authority
		1	2	3			
Oregon	36	0	35	1	73	2.0	1
Oregon	108	9	99	0	207	1.9	2
Michigan	133	4	121	1	249	1.9	3
Florida	34	6	28	0	62	1.8	1
Mississippi	30	9	21	0	51	1.7	4
	341	28	304	2	642	1.9	

1. Walkinshaw (1949); 2. Littlefield and Ryder (1966); 3. Walkinshaw (1965*b*); 4. Valentine and Noble (1970).

and Ryder, 1966), but this is seldom the case with Lesser Sandhill Cranes (*G. c. canadensis*) and does not appear to be common in any North American cranes. In a census of 623 family groups in a total of over 17,500 Sandhill Cranes at Last Mountain Lake, Saskatchewan in the fall of 1972 (Miller and Hatfield, in press), there was only one instance of two young in a family group, and the difference in size and coloration between the young suggested that one might have been adopted (cf. Masatomi, 1972). These data confirmed several years of previous observations in Saskatchewan and Manitoba that migrating pairs of arctic-nesting Sandhill Cranes are seldom accompanied by more than one young.

Novakowski (1966) observed that Whooping Crane nests at Wood Buffalo Park almost invariably contained two eggs, but that shortly after the first egg hatched, the other egg or its chick disappeared. Between 1954 and 1964 an average population of 14 pairs of Whooping Cranes at Wood Buffalo Park produced a total of 61 young that completed their first fall migration, so that annual recruitment was only 0.4 young per pair. Kuyt (1971) recorded the number of eggs in a total of 31 nests between 1967 and 1970 and found that 28 nests contained two eggs, three contained one egg, and about half of the nesting effort was lost each year.

Lack's (1968) hypothesis is that the clutch size of birds has evolved to correspond to the number of eggs from which, on the average, the most young are raised. In nidicolous species, this limit is presumably set by the amount of food the parents can provide for their nestlings. Selection, of course, operates primarily on the number of offspring that survive to reproduce and perpetuate the parental genotype, rather than on the number of eggs laid or the number of young hatched, even though the latter might represent various degrees of energetic waste which would also be subject to natural selection.

If, for example, brood size can be adjusted quickly to correspond to the proximate factor of food availability, natural selection might not produce a close correspondence between clutch size and survival to reproductive maturity, and a few excess eggs during periods of food scarcity might be a reasonable energetic expense compared with the potential advantage of more offspring when food is abundant. This would appear to be the case among raptors, which may raise all of their young to fledging when food is abundant but allow some chicks to starve when food is scarce (Lack, 1966; Southern, 1970).

Many species of large birds, including cranes, lay small clutches of eggs, have long fledging periods and defer breeding until they are two or more years of age. Sandhill Cranes seldom breed until their fourth year (Walkinshaw, 1949) and Whooping Cranes probably defer breeding until at least this age, or possibly older. It is generally agreed (Ashmole, 1971) that deferred breeding is found in populations in which the breeding adults experience difficulty in finding enough food to successfully raise young. Small clutch sizes and long fledging periods are obvious corollaries of this condition. Asynchronous hatching is also characteristic of birds which have difficulty raising young, and is used in various ways to reduce the brood size during periods of food scarcity. As noted earlier, raptors may raise all of their young to fledging when food is abundant, but when food is scarce some or all of the young starve. The Gray Heron (*Ardea cinerea*) normally has a clutch of two eggs but one chick, usually the first hatched, takes the most advantageous position in the nest and gets the most food, and the second chick usually starves to death (Owen, 1955). This behavior also occurs among the Corvidae (Lockie, 1955). This would seem to be a relatively inefficient method of reducing brood size, in that food is wasted on a chick that will ultimately starve, but a clutch size of two provides insurance against the loss of one egg during incubation and also retains the variability which would allow an evolutionary adjustment to more favorable environmental conditions.

Cranes and a few other species that normally lay a clutch of two eggs may also reduce brood size through sibling rivalry among the young. Doward (1962) examined 598 Brown Booby (*Sula leucogaster*) and 98 White Booby (*S. dactylatra*) nests and found only one instance of two chicks surviving in the same nest—in this case both chicks survived together for 34 days before the smaller one died. He often found a second chick beside or near the nest in a weakened condition, and if the second chick was replaced in the nest, it was accepted by the adult but was later found outside the nest, apparently ejected by the larger (usually the older) chick. Vesy-Fitzgerald (1957) found a similar situation in a breeding colony of the Old World White Pelican (*Pelecanus onocrotalus*) in Tanganyika. White Pelicans lay two eggs several days apart but never seem to raise more than one young, and Vesy-Fitzgerald

(1957) observed many instances "of the older chick bullying the younger to death." This behavior seemed to be quite general and he could find no instance of two chicks surviving in one nest.

In his study of Whooping Cranes on their nesting grounds, Novakowski (1966) found that the parents sometimes left the nest with one young shortly after hatching and "all traces of the other egg (other than fragments) disappeared." In two instances in which the parents left the nest with one chick, there was evidence that another chick had hatched, or nearly hatched, but had been destroyed. Observations of captive Whooping Cranes have not been particularly instructive as eggs have frequently been infertile, or have been deliberately or accidentally destroyed by the parents, and chicks that hatched have in most cases succumbed early to disease or predation. More extensive observations have been made of wild and captive Sandhill Cranes. Walkinshaw (1965*a*) observed that Sandhill Crane chicks are extremely aggressive just after hatching, and that the older chick will attack the younger if the parents allow them to remain together. Hyde (1957) noted "time and time again" in wild Sandhill Cranes that the older chick attacked its sibling soon after the second chick hatched, killing it or driving it from the nest. He also found, when clutches of eggs were artificially incubated, that young cranes could not be kept together until they were almost full-grown. Based on the hatching and rearing of over a hundred Sandhill Cranes at the Patuxent Wildlife Research Center, Ray C. Erickson (pers. comm.) has found that young cranes show pronounced antagonism within two days after hatching and this characteristic becomes even stronger by the fourth or fifth day. Aggression becomes so intense that if young cranes are penned together for a few hours, or even less, it is likely that one will be killed. John J. Lynch (personal communication) also found intense sibling rivalry among artifically reared Sandhill Cranes, and suggested that it was unlikely, from his observations, that more than one young would survive in a brood. Erickson (pers. comm.) observed that aggression subsides after about three months (by the time contour plumage is developed) and does not reappear until the cranes are about two or three years old and are approaching breeding age.

DISCUSSION

Although there have been few direct observations of brood size reduction in natural populations of North American cranes, and especially those that nest in rigorous, northern environments, the data that are available from wild and captive birds, and from possibly analogous behaviors in other species with similar breeding characteristics, suggest the following hypothesis: (1) when the first chick hatches it receives the attention of both parents and the second egg is abandoned or destroyed, or (2) if a second egg hatches sibling

rivalry and aggression may lead to the death of one chick. The second chick may die from the attacks of its sibling, or ejection from the nest may cause it to die of exposure to weather, predation or starvation. If this is an innate behavior which is unrelated to the proximate factor of food availability, a second egg may provide insurance against the loss or infertility of one egg, but this reproductive strategy would not permit the species to respond to improved environmental conditions with a corresponding increase in brood size. It would appear, therefore, that natural selection has not eliminated the second egg in clutches of species such as cranes, boobies, and White Pelicans because sibling rivalry is often an efficient method of reducing brood size quickly, and the insurance value of an extra egg is greater than its energetic cost.

SUMMARY

Observations of wild and captive Whooping Cranes and Sandhill Cranes, and apparently analogous behaviors in other species with somewhat similar breeding characteristics, suggest that, although the clutch size of both species is normally two eggs, the brood size is usually reduced to one young because of (1) abandonment of the second egg after the first has hatched, or (2) sibling rivalry which results in the death of the weaker chick. This appears to be an innate behavior which is characteristic of several species, and is unrelated to the proximate availability of food.

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ANATOMICAL NOMENCLATURE FOR BIRDS

The first plenary session of the "International Committee on Avian Anatomical Nomenclature" was held recently at Creighton University School of Medicine, Omaha, Nebraska. Preliminary lists of anatomical terms for all systems were distributed and discussed for five days. After further revision and committee approval, an illustrated list will be submitted for adoption by the World Association of Veterinary Anatomists and publication as *Nomina Anatomica Avium.*

The avian nomenclature committee consists of 60 members representing a wide spectrum of teachers and investigators around the world. (A list of committee members with their addresses is available from the Secretary upon request.)

The next meeting of the International Committee on Avian Anatomical Nomenclature (ICAAN) will be held in Liverpool, England August 2–8, 1974 and the final list will be presented for adoption July 6–12, 1975 at the meeting of the World Association of Veterinary Anatomists in conjunction with the World Veterinary Congress in Thessaloniki, Greece.

The committee welcomes the participation and suggestions of those interested in anatomical nomenclature and solicits illustrations that can be used in the published list. Address correspondence to Dr. John McLelland, Secretary of ICAAN, Department of Anatomy, Royal School of Veterinary Studies, Edinburgh EH9-1QH, Scotland, U.K. or to one of the Chief Reviewers.