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# Cranes of the World: 4. Ecology and Population Dynamics

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# Ecology and Population Dynamics

4 Like other animals, cranes exist as natural populations that are dependent upon particular environmental conditions and that vary in population density between the absolute minimum numbers that have permitted survival to relatively dense populations that may approach or even temporarily exceed the carrying capacity of the habitat. Each species may also have an upper species-typical limit on population density, or "saturation point," which is independent of the carrying capacity of the habitat but which may be determined by such social adaptations as territorial requirements or individual distance characteristics. Within crane populations, individual birds or families remain within home ranges or geographic areas in which their movements are limited and within which they may spend much of their lives. Part of the occupied area may be defended from intrusion by conspecifics for varying periods; these areas of local social dominance range from individual distances to territories and probably play important roles in determining space requirements for crane populations. During periods of the year when breeding or wintering territories are not held, as during migration, dominance hierarchies serve to integrate the activities of the family and flock, and may likewise play important roles in population behavior and ecology. Interspecific differences in morphology and innate behavior patterns may further dictate specific foraging niches for each species, and these too may be of importance in regulating potential population sizes in cranes and in determining competition levels with other species.

Crane populations, whatever their densities, may be analyzed in terms of the individuals that make up the population unit. Thus, their sex composition, as defined by sex ratios, and their age composition, as similarly defined by age ratios, provide important information on the proportion of the population that represents potential breeders. The fall age-ratio, readily determined by field observations, provides critically important information on the rate of recruitment of young birds into the population and thus provides the best possible index to the success of the immediately past breeding season, and thus the maximum rate at which the population may be "harvested" by natural or other means while still maintaining the population size.

This recruitment rate is one of the statistics of importance in estimating the rate of population recycling, which is a result of mortality and survival rates. Mortality and survival are opposite sides of the same coin; as mortality rates increase, the average survival probabilities decrease, and life expectancy (or mean longevity) consequently decreases. Determining mortality rates in crane populations, which are only rarely banded in any numbers, is difficult at best. In rare cases (such as in extremely small populations) it may even be possible to account for every bird, and thus accurate estimates or mortality rates may be obtained for such limited populations. Regardless of the actual mortality rate, all animals in a population eventually die, and the length of time for a virtual 100 percent turning of the population age-class provides another useful population statistic, the turnover rate. In this chapter an attempt will be made to provide estimates of some of these important population characteristics for various cranes.

## Feeding Ecology and Foraging Niches

Rather few species of cranes have been studied intensively as to their foraging niches and how these relate to those of other species of cranes or other possible competitors. As Walkinshaw (1973) has reported, cranes have been observed consuming a wide variety of foods, including frogs, snakes, small birds, birds' eggs, small mammals, snails, crustaceans, small fish, roots, tubers, earthworms, melons, sweet potatoes, insects, and other arthropods, so they clearly have broad dietary requirements. The best available information on foraging ecology comes from various studies on sandhill cranes. Early observations of these species indicated a predominance of vegetable foods in their diets, even on the breeding grounds (Allen, 1952). In an early study of 51 gizzards from lesser sandhill cranes shot during January on their New Mexican wintering areas, Boeker, Aldrich, and Huey (1961) reported that nearly 100 percent of the diet during that period consisted of various types of sorghum grains and green alfalfa.

Studies of sandhill cranes during fall in Saskatchewan (Stephen, 1967) indicate that grain was present in the digestive tracts of 93 percent of 190 specimens. This was predominantly wheat, although barley and oats were also found. The average amount of food found in the gullets was about 27 grams, or only about a fourth of the average amount of wheat and mash consumed per day by captive birds. Foraging density of the birds varied according to distance from their major roosts, and was as high as 248 birds per quarter-section (or 3.8 birds per hectare) in the mile nearest the roost. An average distance of nearly 6 feet was observed between individual cranes foraging in grain fields.

Several other studies have confirmed the general principle that the major foods of sandhill cranes are vegetational materials, including grains, corn, tubers, stems, and leafy matter (table 7). Probably the overall content of such foods, as supplemented by a small amount of animal materials, contains about 10 percent protein (Reinecke and Krapu, 1979). During the spring period in Nebraska it is probable that corn makes up at least 90 percent of the total food consumed (Lewis, 1979a; Reinecke and Krapu, 1979; Iverson, Tacha, and Vohs, 1982). Grain such as ripening wheat is also a major food of fall staging flocks of sandhill cranes in southern Canada (Stephen, 1967), while in the Copper River delta area of Alaska the birds concentrate on the fleshy bulbs of arrow-grass (*Triglochin*)(Herter, 1982).

By comparison, the foraging niche of the larger whooping crane is clearly more closely associated with aquatic foods. During the early winter season in Texas the birds forage almost entirely on blue crabs (*Callinectes sapidus*), which are abundant in flooded tidal flats.

TABLE 7

**Major Foods of Sandhill Cranes at Various Seasons**

| | *Summer (Idaho)** | | *Winter (Texas)†* | | | | *Spring (Nebraska)‡* | |
|---|---|---|---|---|---|---|---|---|
| | *Digestive Tract* | | *Gizzard* | | *Esophagus* | | *Esophagus* | |
| | *Vol. (%)* | *Freq. (%)* | *Vol. (%)* | *Freq. (%)* | *Vol. (%)* | *Freq. (%)* | *Vol. (%)* | *Freq. (%)* |
| Plant Foods | | | | | | | | |
| Timothy (corms) | 68 | 55 | — | — | — | — | — | — |
| Grass (leaves, tubers) | 2 | 10 | tr. | 1 | — | — | tr. | 24 |
| *Lupinus* (seeds) | 1 | 2 | — | — | — | — | — | — |
| Corn (grain) | — | — | — | — | — | — | 93 | 100 |
| Alfalfa (leaves, stems) | — | — | — | — | — | — | tr. | 33 |
| *Cyperus* (underground parts) | — | — | 50.4 | 87 | 38.4 | 61 | — | — |
| *Nymphea* (tubers) | — | — | 8.7 | 9 | 4.8 | 14 | — | — |
| Sorghum (grain?) | — | — | 6.8 | 6 | 37.6 | 11 | — | — |
| Animal Foods | | | | | | | | |
| Orthopterans | 11 | 35 | 2.1 | 9 | 0.2 | 11 | 2 | 27 |
| Dipteran larvae | 6 | 15 | tr. | 3 | 0.1 | 7 | — | — |
| Lepidopteran larvae | 3 | 40 | 6.8 | 9 | 3.9 | 11 | — | — |
| Damselflies | 1 | 30 | — | — | — | — | — | — |
| Beetles | 1 | 40 | 1.8 | 3.9 | 1.3 | 14 | 1 | 84 |
| Earthworms | — | — | — | — | — | — | 3 | 94 |
| Snails | — | — | 2.1 | 5.0 | 2.1 | 11 | 1 | 72 |

*Mullins and Bizeau, 1978 (entire digestive tract, 20 birds).
†Guthery, 1976 (esophagi of 28 birds, gizzards of 70 birds).
‡Reinecke and Krapu, 1979 (esophagi of 34 birds, adjusted for sampling bias).

During December and January these flats and sloughs become drained, and the birds then move into shallow bays and channels to probe for clams of at least six species, and only occasionally consume blue crabs. All the clams and crabs up to about 5 centimeters in width are swallowed whole, while large crabs are pecked into smaller pieces before being swallowed (Derrickson, 1980).

Like the whooping crane, the Siberian crane also consumes aquatic materials, obtained in water 25 to 68 centimeters deep (Sauey, 1979), but its food primarily consists of vegetation rather than animal sources. The demoiselle crane is evidently primarily a terrestrial forager, and extensively consumes ripening cereal grains, chick-peas, and lucerne (alfalfa) (Cramp and Simmons, 1980). The Eurasian crane consumes a diverse array of foods, with plant materials predominating, from the ground, from shallow water, in low vegetation, or from subsurface materials that are extracted by probing (Cramp and Simmons, 1980). The long-billed Australian crane prefers to forage on moist ground, by digging and grazing (Lavery and Blackman, 1969). The sarus crane similarly often digs for food with its bill, but also strips rice grains from their stalks effectively, sometimes kills and consumes snakes up to two feet in length, and otherwise seems to be quite omnivorous (Walkinshaw, 1973). Where it is in contact with wintering Siberian cranes, the sarus crane tends to forage in water no deeper than 30.5 centimeters, but it also contests more shallow areas with Siberian cranes, consistently dominating that species (Sauey, 1979). The African blue crane is apparently a ground-forager, with animal foods perhaps forming the majority of its diet, but it also at times eats grain or seeds and digs up and consumes roots. The crowned cranes also consume grain and grass seeds, but do not seem to dig as much as do the longer-billed species (Walkinshaw, 1973).

## Territoriality and Home Ranges

Apart from breeding territories, which will be considered in the chapter on reproductive biology, cranes also exhibit territoriality outside of the nesting season. Thus the whooping crane exhibits strong winter territoriality, and during that time of year the birds exist as singles, pairs, or, at most, in family parties. Allen (1952) studied winter territoriality at Aransas Refuge and concluded that about 400 acres of salt flats, including ponds and estuaries, are required for the average pair or family of wintering whooping cranes. Of 14 territories actually mapped, the average was 436 acres. All of the 14 had frontage on one or more of the inside bays and included one or more types of salt flat ponds, which apparently are the optimum habitat type. The male is the defender of the territory, while the female and young remain close together and spend much time in foraging.

Nonbreeding territories have not been studied in any detail in the other species, but it seems likely that similar patterns exist in many but not all species. Bieniasz (1979) reported that a flock of 5 to 15 nonbreeding greater sandhill cranes occupied an area having a 3.2 to 4.8 kilometer radius, representing a total home range of several square miles. These birds fed, roosted, and loafed together, indicating that exclusive territoriality evidently was lacking. Walkinshaw (1973) noted that the Japanese crane and the white-naped crane exhibit more severe territorial hostility than does the smaller hooded crane, and besides territoriality associated with nests or young he recognized four additional types of crane territories. These included a crane's "territory around himself" (individual distance maintenance), similar defense of a mate, territories associated with the feeding area (especially during the breeding season), and territories maintained in a flock or at a roost (again perhaps an extension of individual distance attributes).

## Sex Ratios and Age Ratios

The importance of obtaining reliable sex-ratio and age-ratio data in understanding population dynamics of cranes or other bird species is hard to exaggerate. Adult (or tertiary) sex ratios in monogamous species such as cranes should ideally be as close to equality as possible if maximum reproductive efficiency is to be obtained, and age-ratio data are of critical importance in judging the reproductive success for any given breeding season. Since cranes do not exhibit enough sexual dimorphism in size or voice to use reliably for field sexing, it is necessary to use samples of hunter kills to obtain an estimate of such ratios. For example, in a study of 109 lesser sandhill cranes killed on the wintering of New Mexico, the total sex ratio was 59 males to 60 females. If only adult birds are considered, the ratio was 46 males to 50 females. Both comparisons suggest that in this species at least the tertiary sex ratio does not diverge significantly from a 1:1 ratio. In a similar sample of 108 sandhill cranes collected between October and April and representing all three subspecies, Lewis (1979a) found a total of 56 males and 52 females. This also suggests that the adult sex ratio of the species does not diverge appreciably from equality.

A larger sample of age ratios is available from wild crane populations as a result of the relative ease of recognizing juvenile birds in fall crane flocks. The available data (table 8) indicate that the percentages of juveniles in various crane populations range from a minimum of about 8 percent to a maximum of about 18 percent, and average about 13.5 percent for all species. If this can be used as a reliable index of average recruitment rates in wild crane populations, and if the average pair of breeding adults successfully raises a single offspring to the fall period, it clearly means that only about a quarter of the nonjuvenile population of cranes

TABLE 8

**Percentages of Young in Various Crane Populations**

| *Species* | *Percent Young in Population* | *Reference* |
|---|---|---|
| Siberian Crane | 8.5% of estimated 65 birds, 1969 (India) | Walkinshaw, 1973 |
| | 10.2% of 59 birds, 1974 (India) | Sauey, 1976 |
| | 7.3% of 41 birds, 1970s (USSR) | Flint and Kistchinski, 1981 |
| Wattled Crane | 4.2% of 784 birds | Konrad, 1981 |
| Australian Crane | 17% of flocks seen 1968-1970 | Blackman, 1971a |
| Sarus Crane | 16.7% of 137 birds | Blackman, 1971a |
| White-naped Crane | 16.0% of 1,826 birds | Nishida, 1981 |
| Sandhill Crane | | |
| Lesser & Canadian | 7.2% of 2,108 birds, Alaska, 1979-80 | Herter, 1982 |
| | 10.5% of 24,086 birds, Canada, 1975 | Buller, 1976 |
| | 11.5% of 30,393 birds, U.S., 1975 | Buller, 1976 |
| Greater | 11.5% of 2,658 birds, New Mexico | Drewien, 1973 |
| | 11.5% of 14,442 birds, Wisconsin & Indiana | Crete and Grewe, 1982 |
| Florida | 15.6% of 192 birds | Walkinshaw, 1976 |
| Whooping Crane | 17.3% of wintering population, 1938-1952 | Table 29 |
| | 15.1% of wintering population, 1953-1966 | Table 29 |
| | 10.6% of wintering population, 1967-1980 | Table 29 |
| Japanese Crane | 15.2% of 713 birds, 1965-1968 | Walkinshaw, 1973 |
| | 12.8% of 3,339 birds, 1962-1978 | Table 30 |
| Hooded Crane | 13.5% of 3,107 birds | Nishida, 1981 |
| Eurasian Crane | 12.0% of 5,808 birds | Libbert, 1969 |
| | 11.42% of 17,240 birds | Fernandez-Cruz, 1979-1980 |
| | From 5 to 6.7% in various years | Swanberg, 1981 |

represents successfully breeding pairs, with the other 75 percent of adult birds either nonbreeders or unsuccessful breeders. Few if any of the other legally hunted game species in North America have such a low recruitment rate as this, and it poses serious and complex problems of management if cranes are to be legally hunted.

The data in table 8 suggest that there may be substantial inter-population differences in recruitment rates of cranes. For example, the Florida sandhill crane seemingly has a substantially higher recruitment rate than does either the greater or the lesser subspecies. Further, the recruitment rate of the whooping crane has dropped quite substantially since annual counts were first initiated (with the establishment of Aransas National Wildlife Refuge). Possible explanations and implications of this have been discussed elsewhere (Johnsgard, 1982). It seems likely that it may in part be related to the carrying capacity characteristics of the breeding grounds in Wood Buffalo National Park, which seem to support only a rather limited number of breeding pairs in the Sass and Klewi river areas of that park (Novakowski, 1966). Thus, increasing total population size of the species has not been accompanied by a major increase in known breeding birds, which for the period 1968 through 1979 averaged only 32 percent of the total nonjuvenile population (Kuyt, 1981a).

Another way of obtaining information relative to reproductive efficiency in crane populations is to determine the average brood size in populations of cranes with recently fledged young. Except for the crowned cranes, it may be taken as a basic assumption that the average clutch size in cranes is essentially two eggs, and that any family sizes of less than two young can be attributed to mortality of eggs or young among nesting birds. Obviously, such counts do not provide an estimate of those pairs that lost both of their eggs or young, but they do nevertheless provide a potentially useful index to the incidence of mortality among a substantial part of the egg or chick population. As may be seen in table 9, the percentage of pairs leading two fledged young in fall populations ranges from as little as about 11 percent to as high as nearly 40 percent. Thus, year-to-year variations in the raising of one or both youngsters do indeed produce a significant source of variation in annual productivity. The often-repeated statement that "cranes almost never raise more than one youngster" and that the second egg is thus biologically unimportant is therefore clearly subject to argument. For example, before the program of egg-removal from the nests of whooping cranes was instituted, nearly 15 percent of the families arriving at Aransas refuge each fall contained two young. It seems unlikely, however,

TABLE 9

**Average Brood Size and Percent of Fledged "Twins" in Various Crane Populations**

| | |
|---|---|
| Wattled Crane: | Twins have never been reported in wild populations—Konrad, 1981 |
| Sandhill Crane | |
| Lesser & Canada: | 17% of 201 migrant families in the Central Flyway had two young in September (estimated average brood, 1.17 young)—Buller, 1976. |
| Greater (Oregon): | 20.1% of 134 families in September had two young (estimated average brood size, 1.2 young)—Littlefield, 1976. |
| Greater (Idaho): | Average of 1.35 fledged young in 372 families in September (estimated 35% of all families with young)—Drewien, 1973. |
| Greater (New Mexico): | Average of 1.24 young in 282 families, late fall (estimated 24% of all families with young)—Drewien and Bizeau, 1974. |
| Greater (Michigan): | 31% of 324 fall families had two young, or average brood size of 1.31 young per successful pair—Walkinshaw, 1973. |
| Florida: | Three of 27 family groups (11.1%) were groups of 4—Walkinshaw, 1976. |
| Whooping Crane: | 14.5% of 48 broods arriving Aransas, 1949-1963, were of 2 young; average brood size, 1.15 young—Walkinshaw, 1973. |
| Eurasian Crane: | From 20% to 25% over four years; average of 24% or estimated 1.24 young per successful pair—Swanberg, 1981.<br>Of 1,847 pairs, 17.62 percent had two young, or an average brood size of 1.18—Fernandez-Cruz, 1979-1980. |
| Hooded Crane: | 48% of families observed in 1966-67 had two young—Nishida, 1981. |
| White-naped Crane: | 27% of families observed in January 1980 had two young (estimated average brood size, 1.27 young)—Nishida, 1981. |

that this program has directly resulted in the substantial reduction of recruitment rates just mentioned for the species, since the trend began well before the egg-removal program was initiated in 1967, but it has perhaps in a small part contributed to it.

### Mortality and Survival Rates

It has been emphasized that populations of animals can vary in density, in spatial distribution patterns (territoriality favors dispersion, sociality favors clumping), and in sex and age composition. Not only can the population be analyzed for immature and adult components but the adults themselves have age composition characteristics, with the relative frequency of the various age classes depending on the rate at which the animals die. It is possible to gather such mortality information only by marking individuals (preferably while still young enough to determine their exact age at the time of marking), releasing them, and resampling the population at later times to determine how long the marked individuals survive. A review by Farner (1955) provides the theoretical concepts and practical methods that are required in the performance of such investigations with birds, and it is beyond the scope of this short review to mention them here. A few ideas, however, are so basic to the understanding of this aspect of population dynamics that they must be considered individually.

The relative rate at which individuals in a population die is usually expressed as an annual mortality rate (M), which is the ratio of those individuals dying during a year to the number that were alive at the beginning of the twelve-month period, whatever its starting point. The annual survival rate (S) is the opposite ratio: the proportion of the animals still surviving at the end of a twelve-month period to those that were alive at its start. Thus, $S + M = 1.0$ or $S = 1.0 - M$. The total population may be subdivided into different age classes according to the year in which each individual was hatched. The population thus consists of varying numbers of one-year-olds, two-year-olds, etc. For groups banded as birds of unknown ages, the population can alternatively be divided into year classes, representing groups of birds of unknown but varying minimum ages.

The length of time required for an entire age class of hatched young to be essentially eliminated from the population is referred to as the turnover period or turnover rate. This is perhaps properly estimated on the basis of time required for 100 percent of the age class to be reduced to 1 percent of its original size, but practice varies in this regard (Hickey, 1955; Petrides, 1949).

Mortality and survival rates in birds have usually been estimated on the basis of recovery rates of banded birds (Farner, 1955), but this technique requires a sample size large enough to provide a reasonable estimate of mortality rates throughout the entire potential longevity of a species. Banding recoveries often tend to overestimate mortality rates, particularly in long-lived species, where banded birds may survive for longer periods than are desirable for convenient analysis, or where the bands on long-lived birds may wear out and be lost before the birds actually die. Probably both of these conditions exist for cranes in general and introduce biases into the interpretation of banding data.

Until the introduction of legalized hunting of sandhill cranes in the United States in 1961, the intensity of banding activities was low and the incidence of banding recoveries was just about nil. Even as recently as 1977, Lewis commented on the low rate of banding recoveries on sandhill cranes through 1972, with first-year recoveries averaging less than 2 percent and total recoveries no greater than 3.5 percent. In recent years, however, the rate of banding recoveries for this species has increased, and in some cases has exceeded 7 percent (table 10). Thus, of 168 cranes banded in Texas in 1977, 13 had been recovered in three years (7.7 percent). Of 33 total band recoveries from birds banded in Texas through 1979, 26 (79 percent) were recovered within a year of banding. These figures indicate an astonishingly high rate of first-year band recoveries for a species with a presumably very low natural mortality rate, and it is very possible that they reflect a serious degree of hunting overkill of sandhill cranes.

Since so few species of wild cranes have been banded in any numbers, it is only possible to apply the principles of population analysis by banding recoveries to a single species, the sandhill crane. In table 11 a tabulation of banding recoveries of all races of sandhill cranes banded in North America through 1979 and recovered through 1980 is provided. This total of nearly 200 banding recoveries provides a reasonably good basis

TABLE 10

**Some Band Recovery Rates for Sandhill Cranes**

| *Years of Banding* | *Location* | *Birds Banded* | *Bands Recovered* | *Recovery Years* | *Reference* |
|---|---|---|---|---|---|
| 1959-69 | Texas | 134 | 4(3.0%)* | 3—13 | Lewis, 1977 |
| 1965-68 | Nebraska | 542 | 37(6.8%)† | 12—15 | Lewis, 1977 |
| 1977 | Texas | 168 | 13(7.7%)† | 3 | Ramakka, 1979 |

*Recoveries to 1972
†Recoveries to 1981

TABLE 11

**Survival of Sandhill Cranes Based on Banding Recoveries through 1980**

| *Banding Year* | *Years between banding and recovery* 1 | 1-2 | 2-3 | 3-4 | 4-5 | 5-6 | 6-7 | 7-8 | 8-9 | 9-10 | 10-11 | 11-12 | 12-13 | 13-14 | 14-15 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1960 | — | 1 | — | — | — | — | 2 | — | — | — | — | — | — | — | — |
| 1961 | 1 | — | — | 1 | — | — | — | — | — | — | — | — | — | — | 1 |
| 1962 | — | — | — | — | — | 1 | — | — | — | — | — | — | — | — | — |
| 1963 | — | — | — | 1 | — | — | — | — | — | — | — | — | — | — | 1 |
| 1964 | — | — | — | — | — | — | 1 | 1 | — | — | — | — | — | — | — |
| 1965 | 2 | 1 | — | — | 1 | 1 | — | — | — | — | — | 1 | — | — | 1 |
| 1966 | 1 | — | — | — | — | — | — | 1 | — | — | — | — | — | — | — |
| 1967 | 1 | 1 | 1 | 2 | — | — | — | — | 1 | 1 | — | — | 1 | — | |
| 1968 | 9 | 3 | 2 | 2 | 1 | 2 | 2 | 1 | 1 | 3 | 3 | 1 | — | | |
| 1969 | 1 | — | 1 | 3 | — | — | 1 | — | — | — | — | — | | | |
| 1970 | 1 | 2 | — | 1 | 2 | — | 1 | 1 | — | — | — | | | | |
| 1971 | — | — | 1 | — | 1 | — | — | — | — | — | | | | | |
| 1972 | 5 | 2 | 4 | 2 | — | 1 | — | — | — | | | | | | |
| 1973 | 1 | — | 2 | 1 | 1 | — | — | — | | | | | | | |
| 1974 | — | — | — | — | 1 | — | — | | | | | | | | |
| 1975 | 2 | — | — | — | — | — | | | | | | | | | |
| 1976 | 2 | 2 | — | 3 | — | | | | | | | | | | |
| 1977 | 14 | 2 | 1 | — | | | | | | | | | | | |
| 1978 | 30 | 2 | — | | | | | | | | | | | | |
| 1979 | 14 | 1 | | | | | | | | | | | | | |
| Total | 84 | 17 | 12 | 16 | 7 | 5 | 7 | 4 | 2 | 4 | 3 | 2 | 1 | 0 | 3 |

TABLE 12

**Life Table for Wild Sandhill Cranes, Based on Banding Recoveries through 1980**

| *Year Class** | *Total Deaths* | *Deaths / 1,000* | *Survivors / 1,000* | *% Survival* |
|---|---|---|---|---|
| 1 | 84 | 506 | 494 | 49.4 |
| 2 | 17 | 102 | 390 | 79.3 |
| 3 | 12 | 72 | 318 | 81.5 |
| 4 | 15 | 90 | 228 | 71.7 |
| 5 | 7 | 42 | 186 | 81.6 |
| 6 | 5 | 30 | 156 | 83.9 |
| 7 | 7 | 42 | 114 | 73.1 |
| 8 | 4 | 24 | 90 | 78.9 |
| 9 | 2 | 12 | 78 | 86.7 |
| 10 | 4 | 24 | 54 | 69.2 |
| 11 | 3 | 18 | 36 | 66.7 |
| 12 | 2 | 12 | 24 | 66.7 |
| 13 | 1 | 6 | 18 | 75.0 |
| 14 | 0 | 0 | 18 | 100.0 |
| 15 | 3 | 18 | 0 | 0.0 |
| | | | Ave. (years 2-14) | 78.2 |

*Refers to year following banding rather than to the actual age of bird.

TABLE 13

**Estimated Total Sporting Harvests of Sandhill Cranes, 1961-1979***

| *Year* | *Manitoba and Saskatchewan* | *New Mexico* | *Texas* | *Other States* | *Total States* | *Minimum Harvest* |
|---|---|---|---|---|---|---|
| 1961 | — | 542 | — | 2,633 | 2 | 3,146 |
| 1961 (fall) | — | 1,385 | 1,200 | 2,633 | 3 | 2,847 |
| 1962 | — | 1,161 | 1,230 | 2,633 | 3 | 5,087 |
| 1963 | — | 1,064 | 1,230 | 2,633 | 3 | 4,905 |
| 1964 | 3,124 | 1,246 | 1,260 | 2,633 | 3 | 8,263 |
| 1965 | 625 | 631 | 1,350 | 2,633 | 3 | 5,239 |
| 1966 | 531 | 514 | 890 | 2,633 | 3 | 4,568 |
| 1967 | 3,604 | 697 | 1,070 | 2,633 | 4 | 8,006 |
| 1968 | 4,837 | 1,076 | 1,339 | 2,705 | 7 | 9,957 |
| 1969 | 4,444 | 1,212 | 991 | 2,980 | 7 | 9,627 |
| 1970 | 5,344 | 1,805 | 2,213 | 3,185 | 7 | 12,547 |
| 1971 | 2,943 | 2,183 | 3,076 | 8,350 | 7 | 10,790 |
| 1972 | 2,143 | 780 | 2,270 | 3,055 | 9 | 8,284 |
| 1973 | 4,275 | 420 | 7,500 | 3,780 | 9 | 15,975 |
| 1974 | 6,699 | 220 | 4,700 | 3,790 | 9 | 15,899 |
| 1975 | 6,165 | 710 | 7,010 | 4,480 | 9 | 18,365 |
| 1976 | 1,636 | 858 | 6,122 | 2,400 | 9 | 11,016 |
| 1977 | 5,388 | 1,459 | 6,094 | 6,600 | 9 | 19,541 |
| 1978 | 1,575 | 1,089 | 5,720 | 5,300 | 9 | 13,684 |
| 1979 | 3,798 | 1,170 | 5,917 | 5,300 | 9 | 16,185 |

*Excludes cripping losses (about 15 percent of total kill), Canadian native kill, and Siberian and Mexican kills. The 1961-1972 data are from Lewis (1977); 1972-1979 Canadian data are from *Canadian Wildlife Service Progress Notes* 101 (1979) and 115 (1980). U.S. data for 1973-1976 are from Marten (1979), and also exclude Alaskan native kill, estimated at 2,000 birds by Lewis (1977). U.S. data for 1976-1979 are based on information provided by individual states, and include an estimated Alaskan native kill of 2,000 birds. "Total states" represents number of states in which cranes were legal game that year.

for establishing a life table and tentative estimates of annual mortality rates for this species (table 12).

In table 12, the progressively older "year classes" do not represent specific age-classes, since all banded cranes are initially included in "year class" 1, regardless of their actual age. Only a relatively small (12.0) percentage of the total recovery sample comes from birds identified as juveniles or immatures at the time of banding, and most were identified as adult or unknown. By ignoring the results from the year immediately following banding, the effects of presumably higher first-year mortality rates can be eliminated. Even with such an adjustment, the indicated annual survival rates for the species averages less than 80 percent (or more than a 20 percent annual mortality rate), which is well in excess of the recruitment rates indicated for sandhill cranes in table 8. Like the high rate of banding recoveries, these figures strongly suggest that hunting mortality in the sandhill crane is certainly now equalling and probably exceeding the species' current recruitment rates. Similarly, the turnover period of approximately 15 years indicated in table 12 is indicative of annual mortality rates well in excess of the probable 10 to 15 percent recruitment rates suggested by age ratios in fall populations, which should result in a turnover rate well in excess of 20 years (Petrides, 1949).

Because of the recent development of legalized sandhill crane hunting in North America, it is perhaps worth summarizing some of the evidence as to the current harvest levels for that species. The early years of harvest have been summarized by various authors (Johnsgard, 1973; Miller, Hochbaum, and Botkin, 1972; Lewis, 1977), while the years 1966 to 1975 were summarized for each of the states by Marten (1979). Marten observed that during that time period there was an average increase in harvest of sandhill cranes of 8 percent annually, which would represent an approximate doubling of harvest every nine years if current trends continue. He also noted that during an eight-year period of analysis, the state of Texas accounted for 58 percent of the total sport harvest in the United States. An updated summary of estimated legal crane harvests is presented in table 13. To these minimum figures must be added a substantial mortality associated with crippled but unretrieved birds (which is believed to be about 15 percent of the retrieved kill), the kill by Canadian natives (Eskimo and Indian hunters), and the legal or illegal kills in Mexico and in Siberia. Sandhill crane hunting is legal in Mexico and gaining in popularity (Lewis, 1977; Marten, 1979), and a limited amount of hunting also occurs during spring in Siberia. There are no firm bases for judging the sizes of these kills, but 8 of 62 band recoveries from cranes banded in Nebraska have been recovered from Mexico. This would suggest that, in spite of the probable low rate of band reporting from there, probably at least 12 percent of the cranes harvested in the Central Flyway are killed in Mexico. There are still only 4 band recoveries from the USSR (all from the Anadyr Basin), and 3 of these are from birds banded in New Mexico, while the fourth is from a Texas-banded bird. Thus, the Siberian mortality can probably be considered insignificant or at least unmeasurable at present. It thus seems probable that at least an additional 25 percent mortality rate can be attributed to crippling losses and Mexican hunting beyond the reported kills for the United States and Canada, which in the five most recent years of data have averaged about 14,100 birds. If 3,500 birds are thus added to this kill, plus an estimated 2,000 birds killed annually by Alaskan natives, it is apparent that the annual harvest is now probably close to 20,000 birds a year. Given an average fall recruitment rate of approximately 10 percent, it would require a population of 200,000 cranes to replace these losses, not counting all other sources of nonhunting mortality.

The first persons to point out the seriousness of hunting to the sandhill crane population were Miller, Hochbaum, and Botkin (1972), who concluded nearly a decade ago that "further increases in hunting might seriously endanger the species, and that the population is not being monitored accurately enough to detect a major population decline if it did occur." Since then, two additional states have been opened to sandhill crane hunting, and the estimated annual harvest has more than doubled!

The current size of the lesser and Canadian sandhill crane populations (the only ones being hunted legally) is still open to considerable controversy, largely as a result of difficulties in making complete spring inventories. Spring surveys in the Platte Valley of Nebraska have been conducted since 1957 during late March and April, and in most years have averaged about 200,000 birds (Frith, 1974; Lewis, 1979b). The 1976 spring inventory provided a total count of 150,119 birds, but Lewis believed that because of biases in undercounting, the actual population there might have been close to 400,000 birds. This very substantial disagreement underlines the contention of Miller, Hochbaum, and Botkin (1972) that the U.S. Fish and Wildlife Service is increasingly permitting the harvesting of a species of bird with very limited reproductive potential, and on the basis of little knowledge of its actual population sizes or trends. A more recent computer simulation model of cranes by Johnson (1979), using considerably different assumptions than did Miller, Hochbaum, and Botkin, would suggest that the population is not yet being overharvested, but all of these sophisticated models basically must rely on relatively primitive spring census data that are still not adequate to provide faith in such conclusions. Recent data provided by Melvin and Temple (1980) on first-year hunting mortality in sandhill cranes from the area of southern Manitoba cause additional concern about possible overhunting effects. Of 64 birds that were banded in that area (62 juveniles, 2 adults), 9 were shot by hunters during their first fall of life, representing an approximate 14 percent harvest of juvenile birds in this particular population. It is clear that insufficient attention is being paid to sandhill crane harvest rates at the present time. Similarly, Herter (1982) reported that although juveniles made up only 6.5 percent of the young counted in fall flocks of cranes in the Copper River delta area of Alaska, they comprised 21.7 percent of the young in a sample of 46 hunter-killed birds, also indicating a very high vulnerability of juvenile birds to hunting. This figure compares closely with juvenile age ratios in hunter kill samples of 21.9 percent in the 1961 New Mexico season and 22.6 percent in the 1961 Texas season (unpublished report of Texas Game and Fish Commission by A. J. Springs, undated).